



Recent changes in the vegetation of a subarctic fen – implications for carbon dynamics

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<p>Tiivistelmä - Referat - Abstract</p> <p>Ilmastomuutos muuttaa pohjoisten soiden ekohydrologiaa ja hiilen virtoja. Mikäli maaperän kosteus säilyy riittävänä, soiden hiilensidonta saattaa lisääntyä pidentyvien ja lämpenevien kasvukausien seurauksena. Tällöin soiden ilmastoa viilentävä vaikutus tehostuisi. Jos kuitenkin haihdunta kasvaa enemmän kuin sadanta, suot kuivuvat. Tämä taas johtaisi lisääntyviin hiilidioksidipäästöihin ja heikentäisi soiden viilentävää ilmastovaikutusta. Lisäksi soiden metaanivuot riippuvat suurelta osin lämpötilasta ja kosteusolosuhteista. Toistaiseksi ei tiedetä, mitkä ovat soiden toiminnan merkittävimpiä muutoksia ja miten niiden ilmastovaste muuttuu tulevaisuudessa. Tämän tutkimuksen tarkoitus on lisätä ymmärrystä pohjoisten soiden ilmastovasteesta tutkimalla pohjoisen aapasuon viimeaikaista kasvillisuuden kehitystä.</p> <p>Elokuussa 2020 keräsin Suomen Lapista Lompolojängkä-suon reunasta neljä pintaturveprofiilia, joista tutkin viimeaikaiset kasvillisuuden ja hiilenkertymän muutokset. Turve ajoitettiin lyijyisotooppi-menetelmällä. Tuloksissa havaittiin muutos saravaltaisesta kasviyhteisöstä rahkasammalvaltaiseen. Muutoksen alkuhetki ajoittui 1960-luvulle, ja se antaa viitteitä kuivuvista olosuhteista. Kuivumista on raportoitu useilta muiltakin pohjoisilta soilta. Toisaalta vastaavan rahkasammalten yleistymisen on havaittu johtuvan paitsi kosteusolosuhteiden muutoksesta, myös suoraan nousevista lämpötiloista, mitä ei voida poissulkea myöskään Lompolojängkällä. Hiilen kertymä Lompolojängkällä vaikuttaisi kasvaneen kasvillisuuden muutoksen jälkeen, mutta tulosta saattaa kuitenkin vääristää pintaturpeen epätäydellisempi hajoamisaste verrattuna pidemmälle hajonneeseen, syvemmällä olevaan turpeeseen. Lompolojängän keskiosissa, jonne virtaa vettä ympäröiviltä kivennäismailta, ei merkkejä kuivumisesta tai kasvillisuuden muutoksista kuitenkaan havaittu. Näin suuri vaihtelu yhden suon sisällä korostaa suon ilmastovasteen ja hiilidynamiikan monimuotoista luonnetta.</p>		
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<p>Tiivistelmä - Referat - Abstract</p> <p>Global warming is changing the ecohydrology and carbon fluxes of northern peatlands. If the soil moisture level remains high enough, peatland carbon sequestration may increase under longer and warming growing seasons, enhancing the cooling climate impact of peatlands. However, in case the evaporation overcomes precipitation, peatlands will dry. This leads to increased carbon dioxide emissions and the weakening of the cooling climate effect of peatlands. In addition, peatland methane fluxes are regulated by temperature and moisture conditions. What remains unknown, is which changes will be the most prominent and to which direction the climate impact of peatlands will develop in the future. The purpose of this thesis is to gain a better understanding of the peatland climate responses by investigating the recent vegetation development of a subarctic aapa mire.</p> <p>In August 2020, four surface peat cores were collected from the margin of Lompolojänkkä fen in Finnish Lapland. Recent changes in plant communities and carbon accumulation rates were investigated. Pb-210 dating method was applied to establish the chronology. A shift from a <i>Cyperaceae</i>-dominated community into a <i>Sphagnum</i>-dominated community in the beginning of the 1960s was detected. The shift indicates drying habitat conditions. Recent drying has been reported from several other northern peatlands. On the other hand, a similar expansion of <i>Sphagna</i> has been interpreted to be caused not only by hydrological changes but also directly by increasing temperatures, which cannot be ruled out in Lompolojänkkä either. Carbon accumulation in Lompolojänkkä seems to have increased following the change in the vegetation. However, the inferred increase might largely reflect an incomplete level of decomposing characteristic to surface peat. In contrast to the peatland margins, no drying signals or vegetation changes were observed in the central parts of Lompolojänkkä. This variation within a single peatland highlights the heterogeneous nature of peatland climate responses and carbon dynamics.</p>		
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1. Introduction

1.1 Climate change in northern high latitudes

Climate has varied in northern high latitudes (60 – 90°N) during the Holocene, which began ca. 11700 years ago. At the onset of the Holocene, a warming climate trend prevailed in northern high latitudes (Välranta et al., 2015) peaking from approximately 8000 to 5000 years ago at Holocene Thermal Maximum (HTM) (Renssen et al., 2012). Thereafter, excluding short-term warmer phases (e.g. Medieval Climate Anomaly (MCA) approx. 1000–700 years ago (Mann et al., 2009)), a cooling trend has persisted until recently (Marcott, 2013; Zhang, 2017). Since the Industrial Revolution, the atmospheric greenhouse gas concentration – composed of particularly carbon dioxide (CO₂), but also methane (CH₄), nitrous oxide (N₂O), and halocarbons – has increased due to anthropogenic emissions. This has resulted in a global rising trend in the mean surface temperature (Myhre et al., 2013; Fyfe et al., 2013). The temperature increase in northern high latitudes is twice as rapid as the global average and is expected to continue faster than anywhere else on Earth: under RCP 4.5, the global annual mean temperature is predicted to rise approximately 2°C, whereas, in northern high latitudes, the annual mean temperature would rise over 5°C and winter temperatures up to 7°C (Najafi et al., 2015; Overland et al., 2018). This warming is causing further changes, for instance, in hydrological processes. As a consequence of the warming and associated increase in evaporation, precipitation increases in the Arctic region. The mean precipitation is projected to increase 35 – 60% compared to the period between 1986 and 2005, especially during the cold season (Laiñé et al., 2014; Lique et al., 2016; Vihma et al., 2016). The net effect of the future warming and associated hydrological changes on northern ecosystems – such as peatlands – remains unknown (Vihma et al., 2016; Helbig et al., 2020).

1.2 Northern peatlands in the global carbon cycle

Biologically peatland is defined as an ecosystem dominated by peat-producing plants, whereas geologically peatland is defined by peat thickness, usually 30 – 40 cm (Vasander, 1998; Rydin & Jeglum, 2006). Peat refers to soil formed by incompletely decomposed plant and animal remains (Rydin & Jeglum, 2006). Peat accumulation requires a positive effective moisture balance, so that soils may become water-saturated. This results in anoxia, which decelerates decomposition and leads to the accumulation of peat. Cold temperatures further inhibit decomposition (e.g. Gorham, 1991; Rydin & Jeglum, 2006). During the Holocene, climatic

conditions favourable for peat formation have prevailed in northern high latitudes. Northern peatlands have a diplotelmic structure, which means they consist of two layers. The upper layer is well-aerated acrotelm, and the lower layer is permanently water-saturated, anoxic catotelm (Ingram, 1978). The boundary layer between the two fluctuates following the water table depth.

The carbon dynamics of northern peatlands play an important role in the global carbon cycle. Peatland plants sequester atmospheric CO₂ in photosynthesis, part of which is stored in peat, and part of which is released to the atmosphere as CO₂ and CH₄ via plant respiration, decomposition of organic matter (Moore & Knowles, 1987; Gorham, 1991), and fires (Gibson et al., 2018), or lost by leaching (Juutinen et al., 2013). Most of the organic matter is decomposed in aerobic processes in the acrotelm, resulting in CO₂ efflux (Warner et al., 1992). In catotelm, decomposition is slow and conducted by methanogenic bacteria that produce CH₄ (Clymo, 1984; Yrjälä et al., 2011). Peat accumulates when the ecosystem production exceeds the rate of decomposition (Clymo, 1984; Turunen et al., 2002). Since peat consists of ca. 50% carbon, peatlands have formed huge carbon storage over the Holocene (Loisel et al., 2014). According to the most recent estimations, northern peatlands store currently approx. 436 Gt carbon (Loisel et al. 2014), which is significant when compared to that of the atmosphere, which is approx. 800 Gt (Ciais et al., 2013). Peatlands could be described as carbon hotspots: even though they cover only 3% of the global land area, they store up to 30% of the global terrestrial carbon (Scharlemann et al., 2014; Loisel et al., 2014; Xu et al., 2018).

Northern peatlands have contributed to the past changes in climate by regulating the atmospheric greenhouse gas concentrations. As peatlands emit greenhouse gases – particularly CH₄ – and simultaneously accumulate carbon, the net climate impact of a peatland may be either warming or cooling. The net impact depends on the strength of the greenhouse gas fluxes, i.e., the trade-off between carbon sequestration and CH₄ effluxes, and the timescale considered (Whiting & Chanton, 2001; Frolking & Roulet, 2007). CH₄ has a stronger radiative forcing effect than CO₂ (Rodhe, 1990), but CO₂ stays much longer in the atmosphere (Lelieveld et al., 1993). Considering the greenhouse gas fluxes and the properties of the greenhouse gases, most northern peatlands have had a short-term warming impact on the climate at the beginning of their succession, but the effect has eventually shifted into cooling on millennial timescales (Whiting & Chanton, 2001; Mathijssen et al., 2017; Piilo et al., 2020). Northern peatlands initiated during the early Holocene, approx. 10 000 – 8000 years ago (Ruppel et al., 2013) and emitted lots of CH₄, accelerating the orbital-driven early Holocene warming climate trend (MacDonald et al., 2006; Frolking & Roulet, 2007). Simultaneously, peatlands accumulated

peat and formed a carbon stock, which eventually shifted their net impact into cooling (Frolking & Roulet, 2007). Peatland lateral expansion driven by the cool late Holocene climate increased both carbon accumulation and CH₄ emissions to the atmosphere (Korhola et al., 2010), and northern peatlands remain a major natural source of atmospheric CH₄ even today (Neef et al., 2010). However, due to their large carbon storage, northern peatlands currently act as climate cooling landscape elements (Frolking & Roulet, 2007; Mathijssen et al., 2014; Piilo et al. 2020).

1.3 Drivers of the peatland carbon cycle

The carbon cycle of a peatland is affected by both autogenic and allogenic drivers. Autogenic drivers refer to internal peatland processes, whereas allogenic drivers are those external to the peatland system (e.g. Rydin & Jeglum, 2006; Tuittila et al., 2007). Despite this distinction, autogenic and allogenic are interrelated as allogenic factors may affect the autogenic, or autogenic factors override the impact of the allogenic (Rydin & Jeglum, 2006).

1.3.1 Autogenic processes

Autogenic drivers of peatland carbon dynamics include vegetation communities and successional stage (Rydin & Jeglum, 2006). Northern peatlands are often divided into fens and bogs, which differ in their hydrology, nutrient status, pH, vegetation, and carbon fluxes (e.g. Weber 1902 ref. Tuittila et al., 2007; Korhola et al., 1998; Svensson, 1988; Tuittila et al., 2007; Tuittila et al., 2013; Välimäki et al., 2017 and references therein). Peatlands usually initiate as nutrient-rich fens. The peatland succession is related to vertical peat accumulation and typically follows a transition from a nutrient-rich, sedge-dominated fen into a poor fen and eventually into a *Sphagnum*-dominated bog (Rydin & Jeglum, 2006).

Minerotrophic fens receive water and nutrients from the surrounding and/or underlying mineral soil, resulting in a system characterized by high nutrient availability, a high water table, and high pH. Fen vegetation is typically dominated by sedges, minerotrophic *Sphagnum*, and brown mosses (Rydin & Jeglum, 2006). Fens tend to emit more CH₄ than bogs (e.g. Alm et al., 1999; Nykänen et al., 1998; Drewer et al., 2010). This is explained by several reasons. In general, high CH₄ efflux is related to high water table and associated anoxia. (Bergman et al., 1998; Leppälä et al., 2011). Sedges have higher photosynthesis rates than bog vegetation, resulting in higher primary production on fens compared to bogs (Leppälä et al., 2008). High primary production ensures a constant supply of fresh organic matter – a prerequisite for CH₄ production

– mainly easily decomposable sedge litter, part of which reaches the anoxic catotelm as sedge roots (Nykänen et al., 1998; Bergman et al., 1998; Bellisario, 1999; Turetsky et al., 2014). Thus, methanogenic microbes have more favourable conditions in terms of anoxia and nutrition in fens compared to bogs. Besides, many fen species, such as *Carex spp.*, have adapted to the anoxic conditions with hollow aerenchyma-tissues that enable oxygen transport to the roots (Koncalova, 1990). This aerenchyma also forms a pathway for CH₄ to the atmosphere, which prevents CH₄ oxidation into CO₂ while diffusing through the peat layers (Colmer, 2003).

The shift from a fen into a bog in the past can be detected from a peat stratigraphy as a change from sedge peat into *Sphagnum*-dominated peat. Marginal areas of the peatland, however, often maintain minerotrophic conditions (Rydin & Jeglum, 2006). The fen-bog transition occurs when the peat stratum grows thicker, the peatland surface elevates and becomes isolated from the surface- and groundwaters originated from the mineral soil. Thereafter, the peatland receives water and nutrients only from precipitation. Thus, nutrient availability decreases, finally leading to ombrotrophic bog conditions (Rydin & Jeglum, 2006). Typical bog vegetation is dominated by ombrotrophic *Sphagna* but includes also shrubs and some graminoids. *Sphagna* emit acidic compounds to their surroundings, which lowers the pH level down to 4.5 – 3.3 (Clymo, 1964). This further accelerates the success of *Sphagna*, as few other plants tolerate such acidic conditions. The shift from a fen into a bog typically results in decreasing CH₄ emissions and an increasing carbon accumulation rate (Turunen, 2003; Tuittila et al., 2013). Unlike sedges characteristic for fens, *Sphagnum* litter only adds in the acrotelm. Thus, the supply of fresh organic matter into the anoxic catotelm is smaller on bogs than on fens. In addition, much of CH₄ is oxidized into CO₂ by methanotrophic bacteria that thrive on *Sphagnum* (Larmola, 2010), and bog vegetation offers fewer emission pathways for CH₄ than sedge-dominated fen vegetation. This is why bogs emit less CH₄ than fens. Due to the recalcitrant composition of *Sphagnum* litter, its decomposition rate is slower than that of sedge litter, and this explains higher peat accumulation in bogs (Turunen, 2003; Turetsky et al., 2008)

1.3.2 Allogenic processes

Allogenic drivers of the peatland carbon cycle include climate conditions and external disturbances, such as fire and human activities (Rydin & Jeglum, 2006).

Climate is related to the peatland carbon dynamics mainly through temperature and hydrology. An increase in temperature and longer growing seasons may, to some extent, increase carbon

sequestration. However, if plants are exposed to heat and drought stress, warm conditions may also limit their photosynthesis capacity. In addition, ecosystem respiration may also increase in warm conditions (Aurela et al., 2004; Aurela, 2009; Rinne et al., 2020; Heiskanen et al., 2021). Temperature affects also peatland CH₄ emissions by controlling the microbial activity related to both CH₄ production and oxidation (e.g. Bubier & Moore, 1994; Voigt et al., 2017), the latter of which is known to be less temperature-dependent (Dunfield et al., 1993). However, it should be noted that CH₄ dynamics are affected by multiple autogenic and allogenic variables that interact in a complex manner.

Water table level is impacted by climatic factors such as precipitation and, through evaporation, temperature as well as human activity within the catchment. Recent experimental studies indicate that the water table level is a major control of peatland vegetation and carbon dynamics (Mäkiranta et al., 2018; Laine, 2019). Several experiments have shown increasing ecosystem respiration and decreasing CH₄ emissions as a response to the lowered water table, as acrotelm deepens and more aerobic decomposition takes place (Nykänen et al., 1998; Riutta et al., 2007; Ballantyne et al., 2014). High water tables, instead, may increase CH₄ emissions to some extent (Huttunen, 2003).

In general, higher centennial or millennial carbon accumulation rates on northern peatlands have been associated with warm climate periods, such as warm and dry mid-Holocene and MCA (Charman et al., 2013; Loisel et al., 2014). However, also contrasting results have been reported from Northern Fennoscandia (Mäkilä & Moisanen, 2007; Mathijssen et al., 2014) showing a decline in carbon accumulation rates during the HTM. Varying results of the past carbon accumulation rates highlight the significance of spatially inconsistent climate patterns and local factors affecting peat accumulation (Zhang et al., 2018a). For instance, moisture conditions during MCA varied regionally (Linderholm et al., 2018).

During the warm and moist early Holocene, the climatic conditions were favourable for peat formation and vast paludification occurred shortly after ice retreatment (Ruppel et al. 2013). On the other hand, a period of intensive peatland lateral expansion occurred 5000 – 3000 years ago, triggered by the late-Holocene cooling trend. Late Holocene cool climate phases also resulted in permafrost formation on northern peatlands (Treat & Jones, 2018).

1.4 Proposed peatland responses to the ongoing warming

Gallego-Sala et al. (2018) predict an increase in carbon uptake on northern peatlands in the future, indicating a strengthening of the carbon sink and potential for mitigating the global warming. This prediction is supported by an observation of a recent increase in carbon accumulation in Alaska (Loisel & Yu, 2013).

However, carbon accumulation may increase only if the effective moisture remains high enough (Mäkiranta, 2018; Laine, 2019). Laîné et al. (2014) predict that over the northern land regions, precipitation will exceed evaporation during winters, and vice versa during summers. This indicates decreasing soil moisture during growing seasons. Peatland surface drying has been observed recently in many subarctic regions, including Northern Sweden (Galka, 2017), Canada (Piilo, 2017; Bellen et al., 2018) Finland, and Russia (Piilo, 2017; Zhang, 2018b). In addition to the subarctic sites, this trend has been observed also on peatlands in boreal and temperate zones across Europe (Pedrotti et al., 2014; Swindles et al., 2019; Zhang, 2020). In warmer and dryer conditions, ecosystem respiration increases, reducing peatland carbon sinks or turning them into net carbon sources to the atmosphere. This would limit the capacity of peatlands to mitigate future warming and potentially form a strong positive feedback loop that accelerates the current warming (e.g., Gorham, 1991; Limpens et al., 2008). On the other hand, dryer conditions are associated with lower CH₄ emissions (Nykänen et al., 1998; Riutta et al., 2020). Rinne et al. (2020) predicted that peatland drying would have a cooling climate impact for the first 15 – 50 years due to the reduced CH₄ emissions, after which the impact would turn into warming due to increasing CO₂ emissions.

Changes in cryosphere (e.g. permafrost thaw and decreasing snow cover duration), as well as regional variation in both climate predictions and landscape characteristics, make hydrological changes and associated carbon cycle changes challenging to predict (Laîné et al., 2014; Conner et al., 2016). Furthermore, changes in vegetation as a response to altered climate and hydrology complicate the predictions of the peatland carbon cycle and feedback mechanisms (Mäkiranta et al., 2018). In addition to the direct impacts, water table decline may also trigger the autogenic peatland processes and disturbance dynamics that may further alter the carbon cycle. Ombrotrophication may be accelerated as lowering water table isolates the peatland surface from minerotrophic water sources and the fen-bog transition has been observed to have occurred within decades (Tahvanainen, 2011; Loisel & Yu, 2013; Bellen et al., 2018). The

enhanced fen-bog transition could accelerate carbon accumulation and have a cooling climate impact (Loisel & Yu, 2013).

1.5 Peatland plant macrofossils as paleoindicators

As peat accumulates *in situ*, a peat column forms a vertical archive of the local vegetation history (Birks et al., 2013). Peat consists mainly of plant macrofossils: remains of plant material visible to the naked eye. The minimum size of a plant macrofossil has been determined to 0.5 mm. Peatland plants are adapted to certain environmental conditions, thus their remains can be used as indicators for past temperature (Kultti et al., 2004), moisture conditions (Väliranta et al., 2007), and successional history (Tuittila et al., 2013) of the peatland. As plant communities are associated with certain carbon fluxes, plant macrofossil data can also be used to infer the past carbon dynamics and the radiative forcing effect of the peatland (e.g. Mathijssen et al., 2014).

1.6 Research objectives and hypotheses

Changes in the global peatland carbon cycle have been recognized as a poorly understood feature in the current climate models (Loisel et al., 2020). Peatlands contain a significant amount of carbon, and they are capable of fixing, storing, and releasing it. Thus, peatlands have a great potential for both mitigating and accelerating the current climate warming and they require more attention from the scientific community. For a number of reasons, it is particularly essential to gain a better understanding of how northern fens are responding to the ongoing climate change. Firstly, fens remain a common peatland type in rapidly-warming subarctic areas. Secondly, their contribution to the atmospheric CH₄ concentrations is significant (Treat et al., 2021). Thirdly, fens are more sensitive to climate changes than bogs (Gong et al., 2013; Kokkonen et al., 2019).

The purpose of this project is to gain a better understanding of how the carbon cycle of northern fens is changing due to the current climate change. My thesis contributes to several ongoing projects, in which the response of the vegetation, moisture status, and carbon accumulation of subarctic fens and boreal bogs to the recent climate change are investigated.

Finnish Meteorological Institute has conducted continuous greenhouse gas measurements on a fen called Lompolojänkki in Northern Finland since 2006. According to still unpublished data,

there is some indication of a slight decrease in the annual net CO₂ uptake due to increased respiration. This could potentially be attributed to the recent warming and/or changes in the vegetation coverage and leaf area (Lohila et al., 2018). I will investigate whether there are recent changes in the plant community and carbon accumulation rate at Lompolojänkkä mire margins, which are known to be sensitive for changes in environmental conditions. My aim is to produce a high-resolution reconstruction of recent paleovegetation and assess the drivers behind the potentially found vegetational changes by comparing them with palaeoclimatological data from the site.

My research questions are:

- 1) Has the vegetation changed at Lompolojänkkä mire margins during the past decades?
- 2) How has the carbon accumulation rate at Lompolojänkkä mire margins changed during the past decades?

2. Materials and methods

2.1 Study site and fieldwork

The study site is a subarctic fen called Lompolojänkkä. It is located in Finnish Lapland, 150 km north of the Arctic Circle, in Pallas-Yllästunturi National Park, near to Pallas-Ounastunturit fell chain and in the catchment area of Lake Pallasjärvi (N67°59.835', E24°12.546') (Figure 1). The area belongs to the northern aapa mire region. The average temperature in the area is -1.4°C (1981 – 2010) and the mean annual precipitation 484 mm (Pirinen et al., 2012).

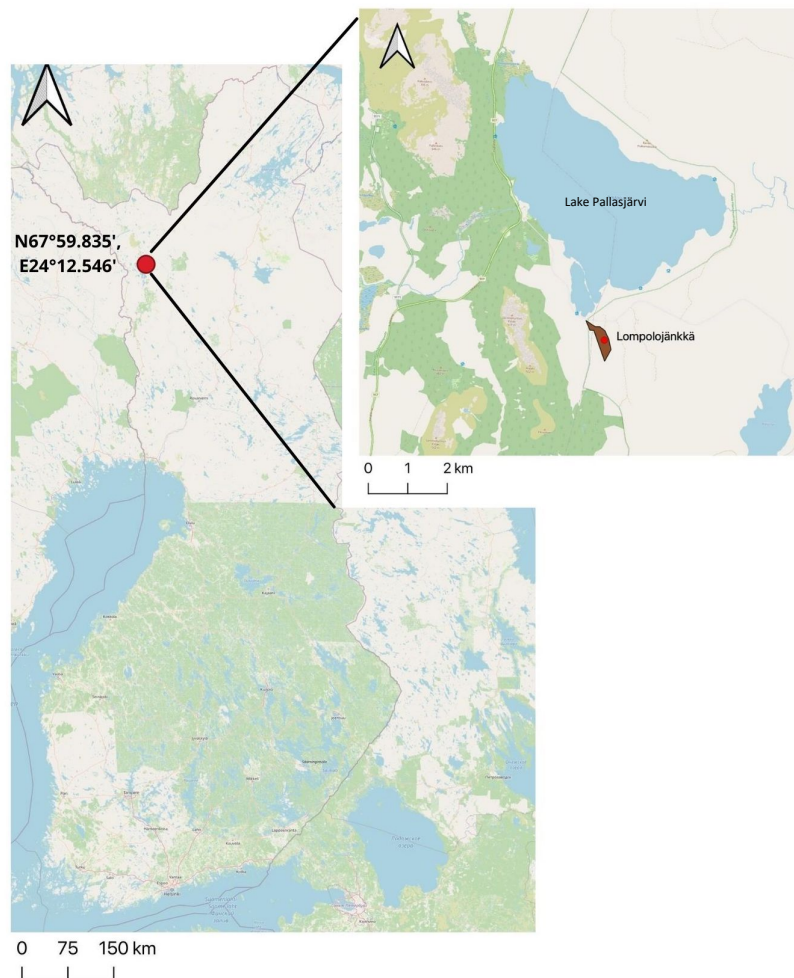


Figure 1. The location of Lompolojänkkä.

Lompolojännkä is an open, eutrophic fen (Figure 2). Its hydrology is highly affected by a small stream that flows through it. The peatland initiation began nearly 10 000 years ago. To the present, 2.5 metres of peat has accumulated (Mathijssen et al. 2014). The current vegetation varies according to the moisture gradient: *Salix lapponum* is highly abundant around the stream, whereas most of the fen is dominated by *Carex* spp. (e.g. *Carex lasiocarpa*, *C. rostrata*, *C. canescens*) and herbs (e.g. *Comarum palustre*, *Menyanthes trifoliata*). The moss cover is discontinuous, characterized by fine-scale variation, and dominated by minerotrophic peat mosses, such as *Sphagnum riparium*, *S. teres*, *S. warnstorffii*, *S. subsecundum*, and *S. fallax* (Aurela et al. 2009, Drewer et al. 2010, personal observation 2020). Some eutrophic brown mosses, such as *Scorpidium* spp., are also found (personal observation, 2020). In marginal areas, however, the species composition is different compared to the central fen area. As typical to aapa mires, marginal areas dryer and more oligotrophic, characterized by shrubs, *Sphagnum fuscum* and *Sphagnum warnstorffii* (Table 1; personal observation, 2020; Rydin et al., 1999).



Figure 2. General view of Lompolojännkä fen and fell Lommoltunturi. (Photo: Olivia Kuuri-Riutta 2020).

Table 1. Current vegetation on the coring points.

Coring point	Feature	Water table depth (positive value = below ground surface)	Species
1	Hummock	26 cm	<i>Andromeda polifolia</i>
			<i>Empetrum nigrum</i>
			<i>Equisetum palustre</i>
			<i>Eriophorum vaginatum</i>
			<i>Rhododendron tomentosum</i>
			<i>Rubus chamaemorus</i>
			<i>Sphagnum fuscum</i>
			<i>Vaccinium oxycoccos</i>
2	Lawn	9 cm	<i>Andromeda polifolia</i>
			<i>Carex pauciflora</i>
			<i>Eriophorum vaginatum</i>
			<i>Rubus chamaemorus</i>
			<i>Sphagnum fuscum</i>
			<i>Vaccinium uliginosum</i>
3	Hummock	25 cm	<i>Andromeda polifolia</i>
			<i>Carex pauciflora</i>
			<i>Empetrum nigrum</i>
			<i>Eriophorum vaginatum</i>
			<i>Rubus chamaemorus</i>
			<i>Sphagnum fuscum</i>
			<i>Sphagnum warnstorffii</i>
			<i>Vaccinium uliginosum</i>
4	Lawn	15 cm	<i>Andromeda polifolia</i>
			<i>Aulacomium palustre</i>
			<i>Carex pauciflora</i>
			<i>Empetrum nigrum</i>
			<i>Eriophorum vaginatum</i>
			<i>Equisetum palustre</i>
			<i>Rubus chamaemorus</i>
			<i>Sphagnum angustifolium</i>
			<i>Sphagnum warnstorffii</i>
			<i>Vaccinium oxycoccos</i>
			<i>Vaccinium uliginosum</i>

The peat at the central fen was too wet and the peat matrix was too loose for coring. Instead, four coring points were chosen from the marginal area of the peatland, where the peat was suitable for coring (Figure 3). Therefore, all coring points were located in the aapa mire margin that represents a transition between the fen and the forest edge. However, all four coring points were cored from slightly different surfaces (Table 1). The use of multiple study points is often necessary to capture any internal variation in the past vegetation (e.g. Mathijssen et al., 2014; Piilo et al., 2020).



Figure 3. Coring site at Lompolojännkä.

Coring points 1 and 2 were situated at a 120 cm distance from the edge of the central fen. Coring point 1 represents a relatively high hummock. The current vegetation at the coring point is characterized by *Sphagnum fuscum* and a relatively high abundance of shrubs, such as *Andromeda polifolia*, *Empetrum nigrum*, *Rhododendron tomentosum*, and *Vaccinium oxycoccos*. *Rubus chamaemorus* is also present (Table 1, Figure 4 a). Coring point 2 (Figure 4 b) was a high lawn dominated by a dense *Sphagnum fuscum*-carpet, near coring point 1. Shrubs were present, but their coverage was scarcer compared to the coring point 1. Coring point 3 (Figure 4 c) is a low hummock situated a few metres from the edge of the surrounding forest.

The moss layer consists of *Sphagnum fuscum*, and at the edge of the hummock, *Sphagnum warnstorffii*. *Empetrum nigrum* and *Rubus chamaemorus* are the most abundant vascular plant (Table 1, Figure 4 c). Coring point 4 (Figure 4 d) represents a high lawn situated near the coring point 3. The moss layer is dominated by *Sphagnum warnstorffii*, however, some *Aulacomium palustre* and *Sphagnum angustifolium* are also present. The most abundant shrub is *Vaccinium uliginosum*.



Figure 4. Coring points from above. a: Coring point 1, b: Coring point 2, c: Coring point 3, d: Coring point 4.

The fieldwork took place in September 2020. I used a box corer to collect the peat samples (Figure 5). The cores were visually analysed on the field, after which they were wrapped in plastic and packed in plastic tubes for transportation.



Figure 5. A box corer was used to collect the peat profiles.

2.2 Dating

Lead (Pb-210) dating method was used to establish the chronology for the peat profiles. Due to the strict timetable for graduation, only Core 2 was dated. The peat core was dated at 1 – 2 cm resolution. I prepared the samples by drying them at 80°C for 48 hours and then grinding them for the Pb-210-analyses. I also assisted Susanna Salminen-Paatero at the Department of Chemistry in preparing the samples for lead dating by performing polonium precipitations, as spontaneous electrodeposition of Po on silver discs.

Pb-210 is a radioactive isotope of lead, forming naturally as a decay product of radon Rn-222 in decay series of uranium U-238. It is deposited on land from the atmosphere (Krishnaswamy et al., 1971). Pb-210 decays into polonium Po-210 with a half-life of 22.3 years, and further into stable lead isotope Pb-206. Pb-210 dating is based on measuring the activity of Po-210 throughout the peat profile (Krishnaswamy et al., 1971; Appleby & Oldfield, 1978; Turetsky et al., 2004). Pb-210 dating is suitable for dating samples younger than 150 – 200 years. Uncertainties in Pb-210 dating are related to post-depositional mobility i.e. vertical movement of Pb-210 in the peat column (Turetsky et al., 2004).

2.3 Plant macrofossils

Plant macrofossils were analysed according to the Quadrat and leaf count protocol (QLC) first introduced by Barber et al. (1994) and further developed by Välranta et al. (2007). Each peat core was analysed at 4 cm resolution, and 1 cm resolution where significant changes in plant assemblages were detected. Subsamples of 5 cm³ were taken from each 1 cm thick slice and cleaned with a 140 µm sieve. No chemical treatment was necessary. The retaining remnants were placed in a transparent Petri dish with 2 – 3 mm water, and the proportion of each peat component was determined by estimating the coverage of each plant group by examining the samples systematically under a stereomicroscope. *Sphagnum* species were identified further to species level using a light microscope: a random selection of approximately 100 *Sphagnum* leaves was identified and the results expressed as percentages of the total proportion of *Sphagnum*. Leaves and seeds were counted separately and expressed as counts. Examples of plant macrofossils are presented in Figures 6 a – g.

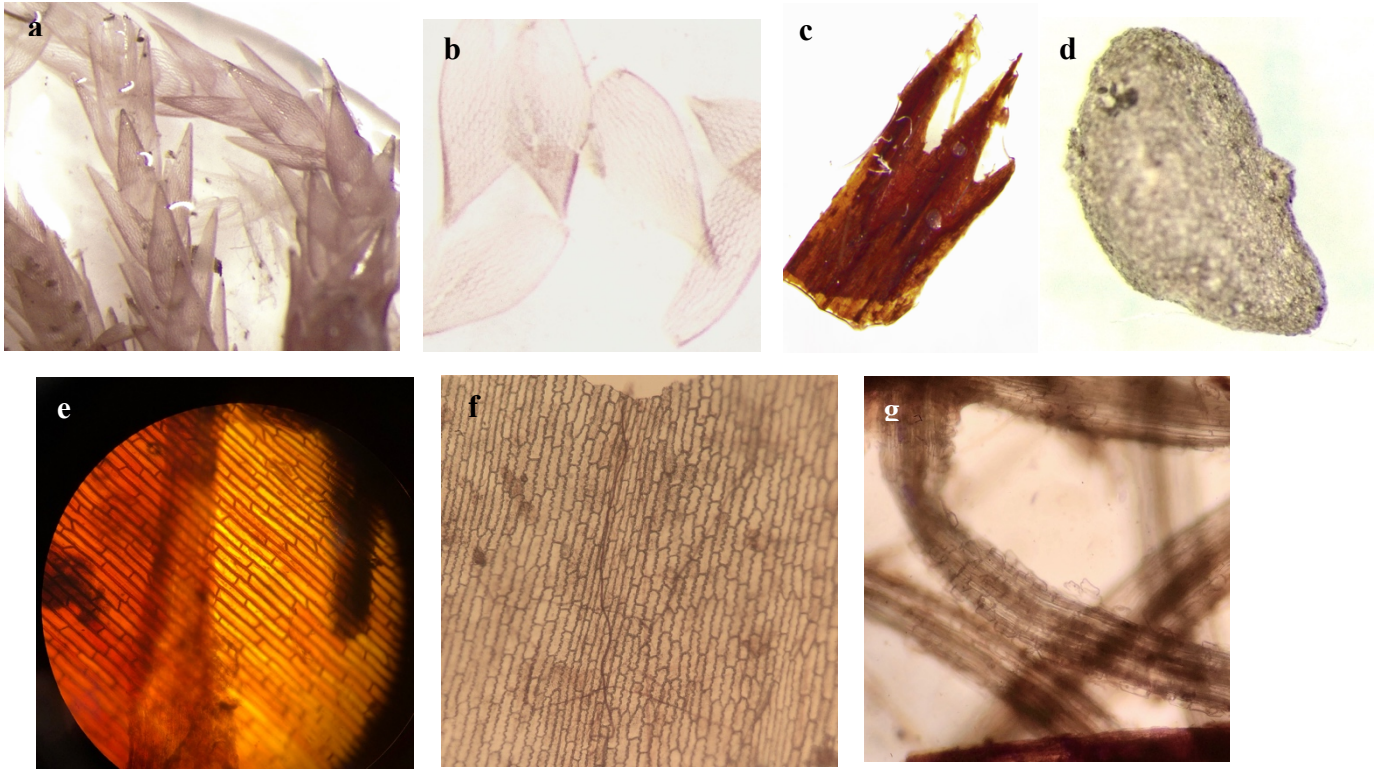


Figure 6. Examples of plant macrofossils. Photos a-d are taken through a light microscope and photos e-g through a stereo microscope. a: *Sphagnum warnstorffii* branches. b: *Sphagnum warnstorffii* branch leaves. c: *Equisetum* sp. d: *Empetrum nigrum* seed. e: *Equisetum* sp. cells. f: *Eriophorum vaginatum* cells. g: *Carex* sp. root cells.

2.4 Carbon accumulation

The carbon accumulation rate was calculated for Core 2 in a 1 cm interval. Apparent Carbon Accumulation Rate (ACAR) ($\text{g/m}^2\text{y}^{-1}$) can be calculated using the following function

$$\text{ACAR} = p \times d \times C \times 1000$$

where p is peat accumulation (m/y^{-1}), d is peat bulk density (g/m^3), and C is the carbon content of peat (Turunen et al., 2001; Turunen et al., 2002). In addition, Recent Apparent Carbon Accumulation Rate (RERCA) was calculated. The following function was applied:

$$\text{RERCA} = c/a$$

where c is cumulative carbon accumulation and a is the bottom age of the considered section.

The peat accumulation rate is achieved by dividing the peat thickness by years. For the bulk density, I prepared volumetric samples of 5 cm^3 of fresh peat, after which the samples were dried at 90°C for four hours and weighted when fully dried. The weight of the plastic container

was estimated based on the measured average weight of 100 containers, and the container weight was subtracted from the total weight. The bulk density values were obtained by dividing the dry weight with the fresh volume. Peat carbon content was investigated by conducting a C/N (carbon/nitrogen) analysis with Leco TruSpec Micro CHNS at the Department of Environmental Sciences, University of Helsinki. Carbon content was estimated only at a 2 cm interval, so for every second centimetre, the C and N value was calculated as the mean of the sample above and below. The carbon-nitrogen ratio (C/N-value) was calculated by dividing the carbon content by nitrogen content in each sample.

3. Results

3.1 The chronology

Core 2 was dated with the Pb-210 dating method. Lead activity in different depths is presented in Figure 7. Detectable lead activity originating from atmospheric deposition was found until the depth of 20 cm. Below that, only so-called supported lead activity, that occurs in soils independently of atmospheric deposition, was detected. Therefore, samples below 20 cm have no age. The oldest dated sample, at 18 – 20 cm, was dated to 245 years (Figure 8).

Between the years 1832 and 1922, only one cm of peat has been accumulated. It is notable that, according to Figure 8, also between the years 1944 and 1946, one cm of peat was accumulated. This is a rather unrealistic value for two years, particularly because it is not in the surface and it differs from the general pattern.

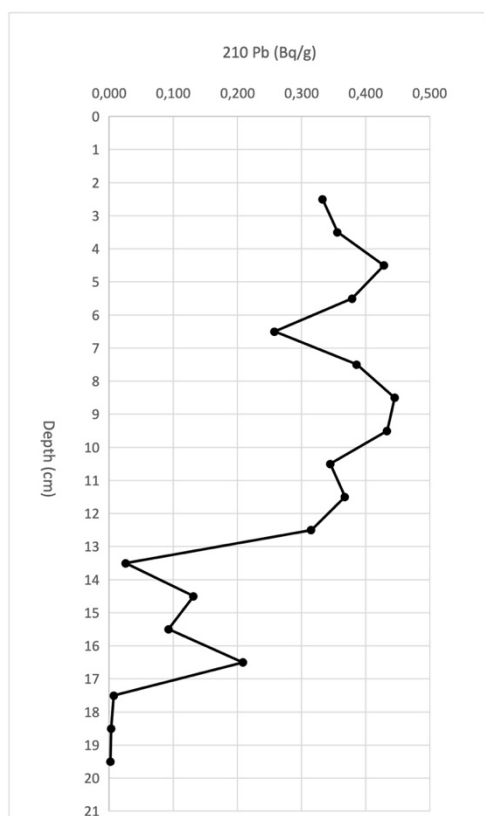


Figure 7. Pb-210 activity (Bq/g) in different depths in Core 2.

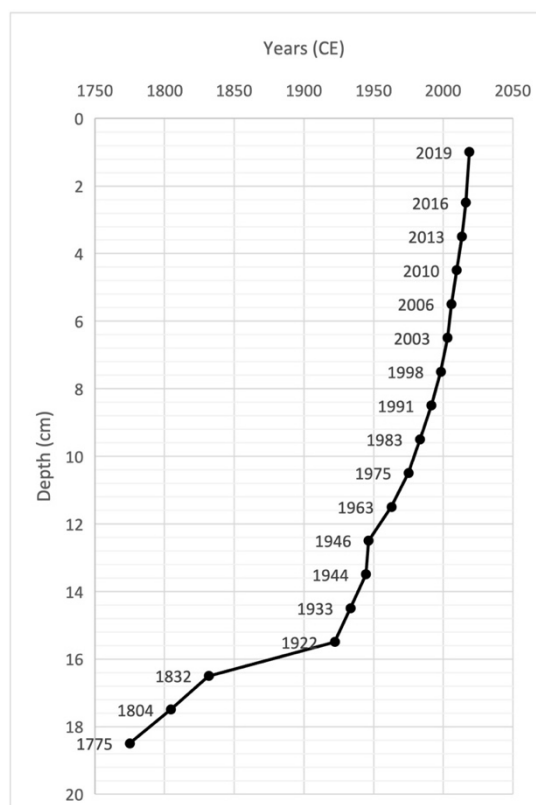


Figure 8. Depth and the corresponding year in Core 2.

3.2 Changes in the vegetation composition

The total number of the identified taxa was 22, most of which were identified to the species level. However, there were some exceptions. For instance, sedge roots are impossible to identify to the species level without any additional information. *Sphagnum*-mosses were identified to the species level whenever stem leaves were present. Based on the branch leaves, colour, and the overall habitus, two species were identified to the species level with uncertainty and thus marked as “cf.”. All the taxa are listed in Table 2.

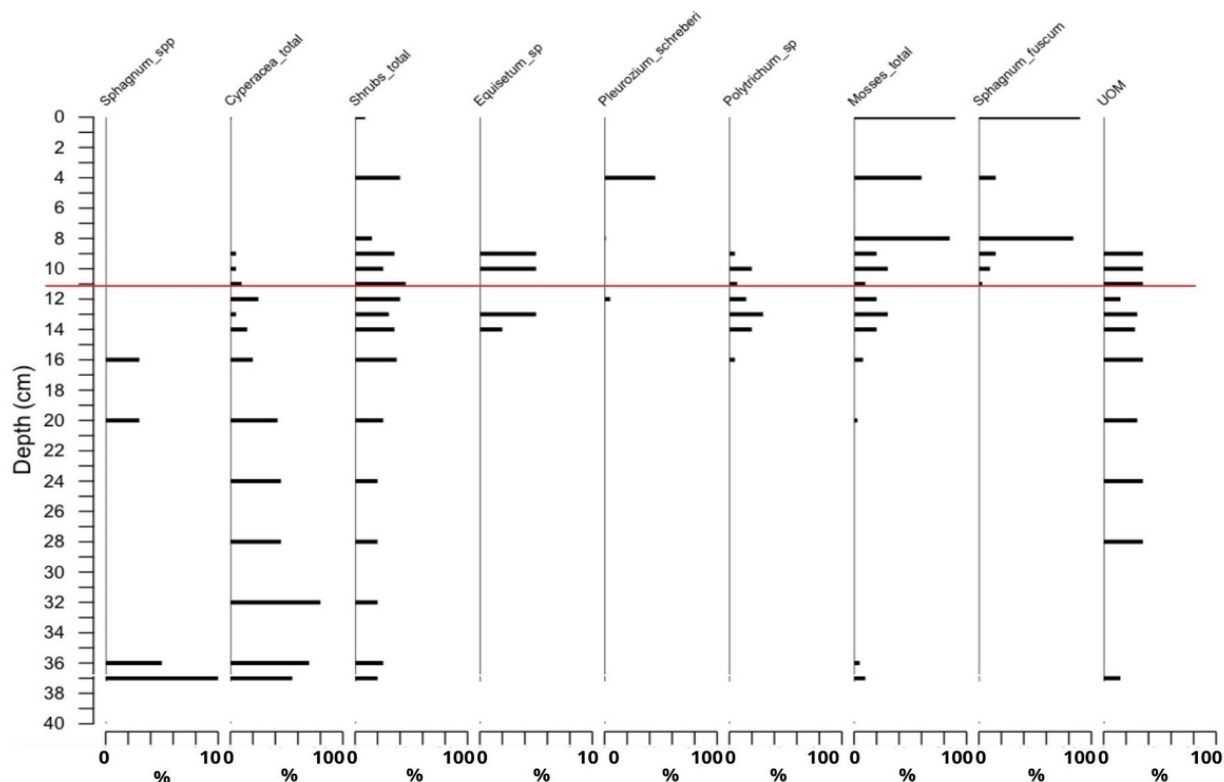
Table 2. All taxa identified in the data from all cores.

Plant group	Species
Mosses	<i>Bryum sp.</i>
	<i>Calliergon sp.</i>
	<i>Mylia anomala</i>
	<i>Pleurozium schreberi</i>
	<i>Polytrichum sp.</i>
	<i>Sphagnum angustifolium</i>
	<i>Sphagnum fuscum</i>
	<i>Sphagnum cf. capillifolium</i>
	<i>Sphagnum cf. majus</i>
	<i>Sphagnum warnstorffii</i>
	<i>Straminergon stramineum</i>
Cyperaceae	<i>Carex spp.</i>
	<i>Carex pauciflora</i>
	<i>Carex cf. magellanica</i>
	<i>Eriophorum vaginatum</i>
Shrubs	<i>Andromeda polifolia</i>
	<i>Betula nana</i>
	<i>Empetrum nigrum</i>
	<i>Vaccinium oxycoccos</i>
	<i>Vaccinium uliginosum</i>
Others	<i>Equisetum sp.</i>
	<i>Rubus chamaemorus</i>

All four cores indicate a similar, rather rapid shift in the vegetation composition (Figures 9 – 12). The lower parts of all cores consist of sedge peat representing typical fen vegetation: the peat is characterized by a high abundance of *Cyperaceae* -remains, and only a few moss and shrub remains. The moss remains are mainly *Sphagna*, however, in Core 4 (Figure 12) the moss species include *Calliergon sp.*, *Sphagnum cf. majus*, and *Straminergon stramineum*. Also, occasional *Empetrum nigrum* seeds were found, which indicates that hummocks without prolonged waterlogging have been present (Mauquoy & van Geel, 2013). Between 20 and 5 cm, the share of mosses increases, whereas *Cyperacea* nearly disappears. The transition from sedge peat to *Sphagnum*-peat occurs within 1 – 5 cm peat section, leading to the conclusion that the change has likely been a rapid shift rather than a result of a gradual development (Figures 9 – 12). According to the dating results from Core 2, the vegetational shift occurs in the 1960s (Figures 8 & 10).

Towards the surface, the peat is dominated by *Sphagna* and a few other moss taxa. In Core 1, a *Polytrichum*-phase precedes the invasion of *Sphagnum fuscum*, and in Cores 1 and 2 *Pleurozium schreberi* appears shortly after with high abundance (Figures 9 & 10). In Core 2, the *Pleurozium schreberi* -phase occurs from the 1980s to the 1990s. In Cores 1, 2, and 3, the current dominant species is *Sphagnum fuscum*, whereas in Core 4 it is *Sphagnum warnstorffii* (Figures 9 – 12). The proportion of unidentified organic matter (UOM) decreases towards the surface, indicating a lower humification rate.

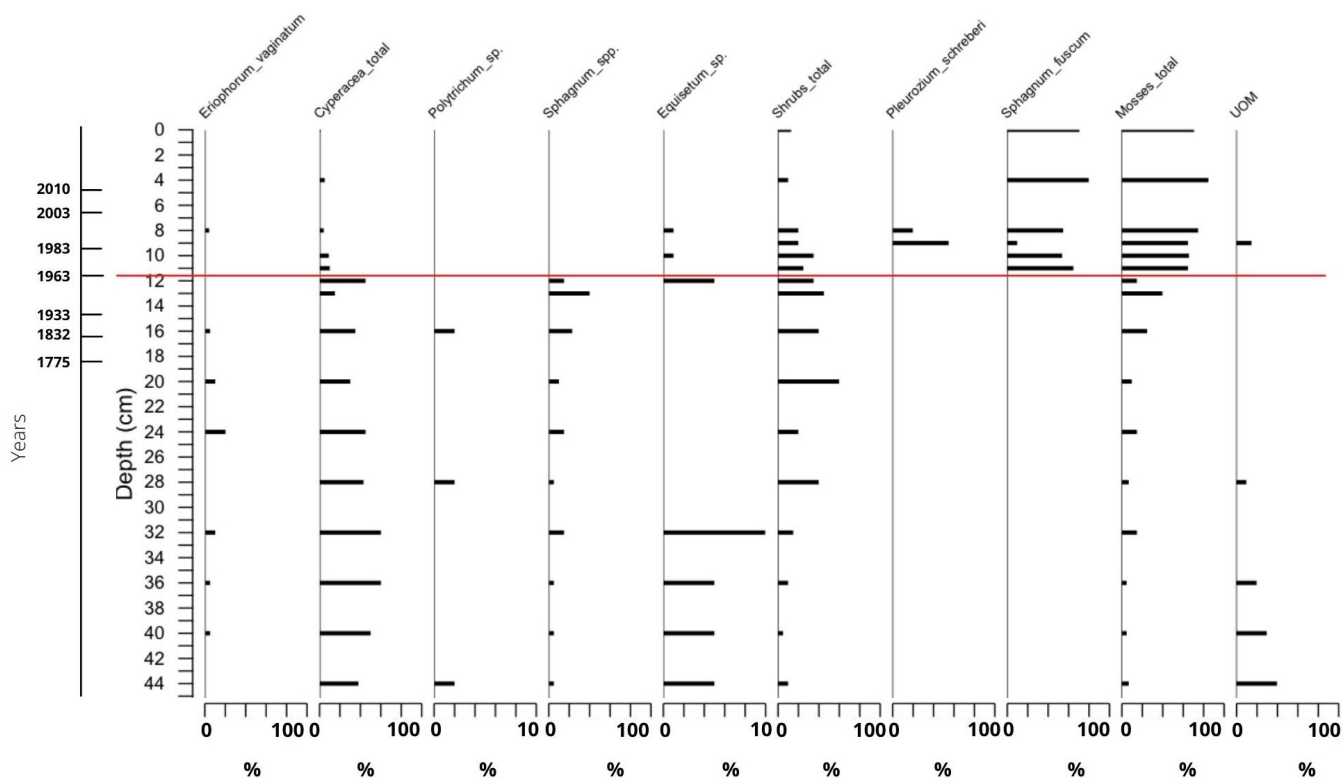
Lompolojännkä plant macrofossil assemblages of Core 1 Selected taxa



Analyst: O. Kuuri-Riutta

Figure 9. Plant macrofossil stratigraphy in Core 1. Note the varying scale on the x-axis: 0-10% or 0-100%. The red line indicates the transition from sedge peat to Sphagnum peat.

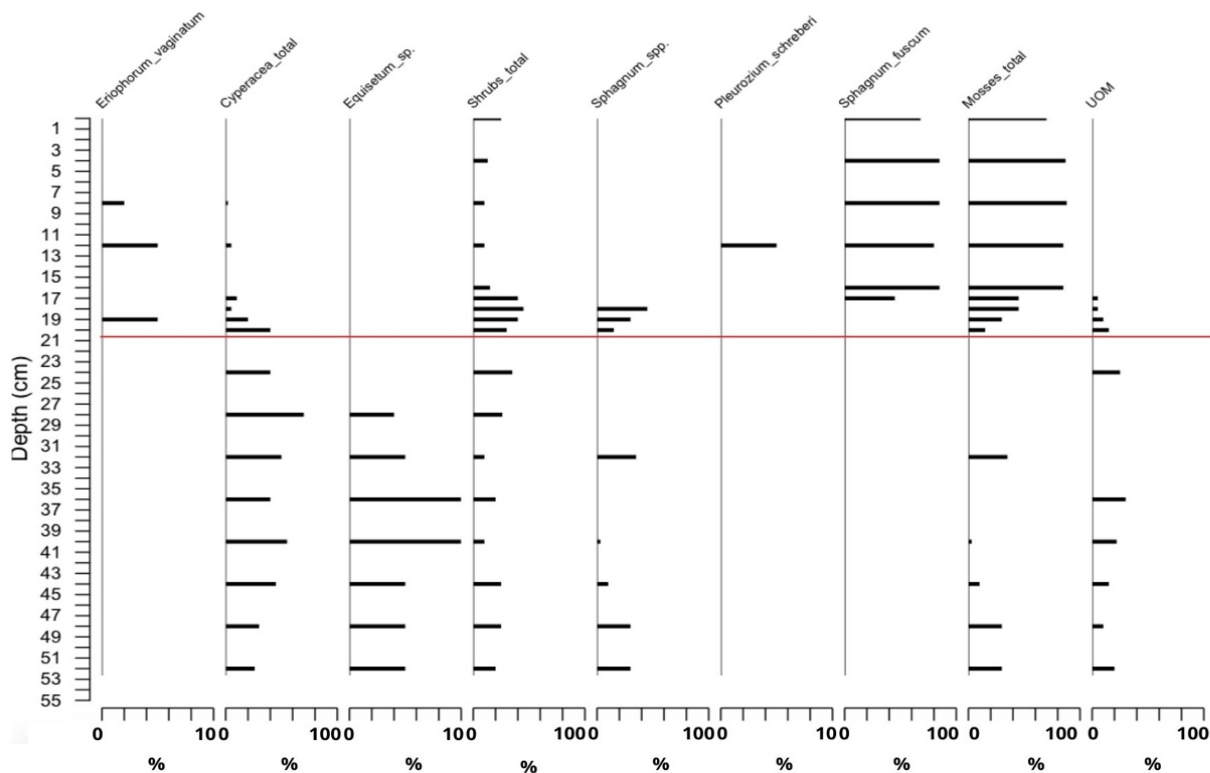
Lompolojännkä plant macrofossil assemblages of Core 2 Selected taxa



Analyst: O. Kuuri-Riutta

Figure 10. Plant macrofossil stratigraphy in Core 2. Note the varying scale on the x-axis: 0-10% or 0-100%. The red line indicates the transition from sedge peat to Sphagnum peat.

Lompolojännkä plant macrofossil assemblages of Core 3
Selected taxa

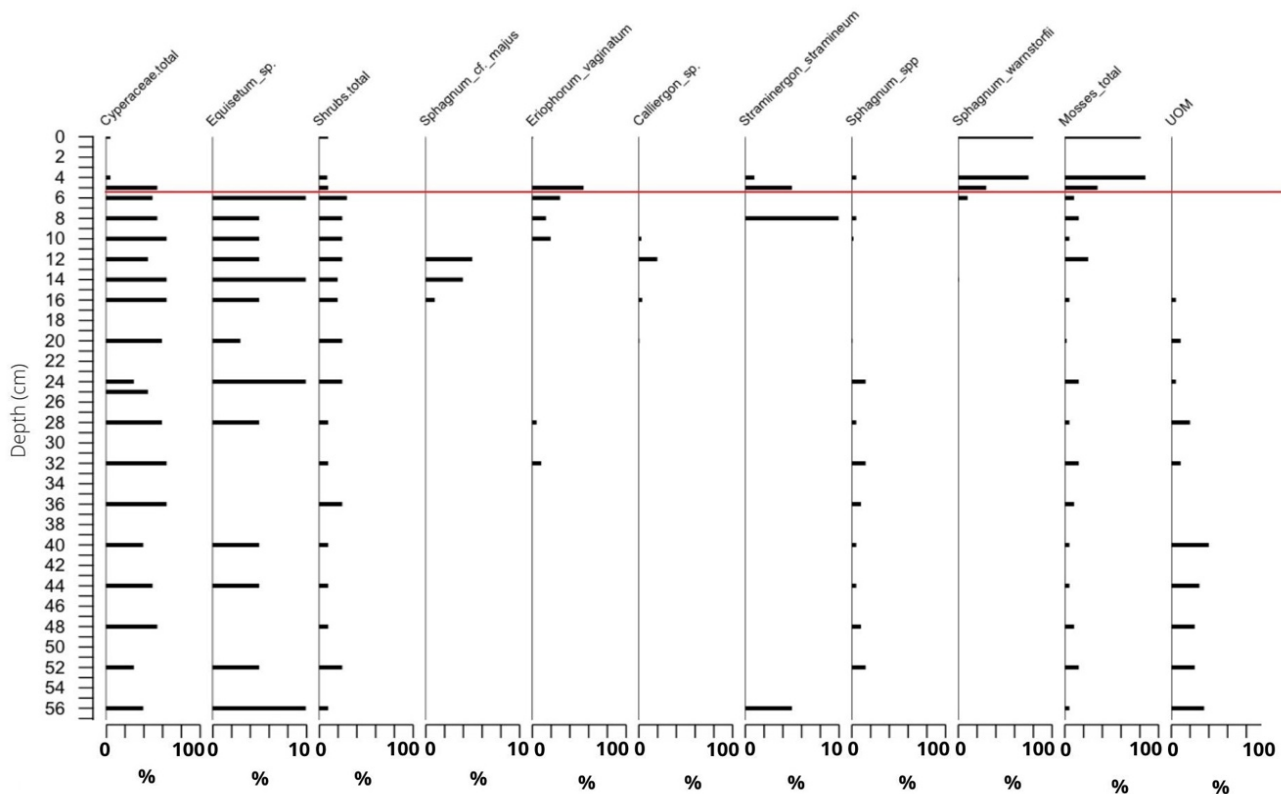


Analyst: O. Kuuri-Riutta

Figure 11. Plant macrofossil stratigraphy in Core 3. Note the varying scale on the x-axis: 0-10% or 0-100%. The red line indicates the transition from sedge peat to Sphagnum peat.

Lompolojännkä plant macrofossil assemblages of Core 4

Selected taxa



Analyst: O. Kuuri-Riutta

Figure 12. Plant macrofossil stratigraphy in Core 4. Note the varying scale on the x-axis: 0-10% or 0-100%. The red line indicates the transition from sedge peat to Sphagnum peat.

3.3 Peat properties

In all four cores, peat bulk density is declining towards the surface (Figure 13), whereas the C/N ratio increases following the vegetation change (Figure 14). Bulk densities vary between approx. 0,03 and 0,14 g/cm³. In Core 1, a steep bulk density decline is visible from 5 cm to the surface, which is 3 cm above the change in the peat type from sedge peat to Sphagnum peat. In Core 2, a steep decline occurs between 9 and 7 cm, also a few centimetres above the peat type change. In Core 3, such a rapid decline in the bulk density is not visible in the topmost 10 cm, but the decline is more gradual and appears as a longer-term trend. In Core 4, a drastic decline occurs between the depths 7 and 3 cm, covering the peat type change (at 5 cm) but beginning already below it.

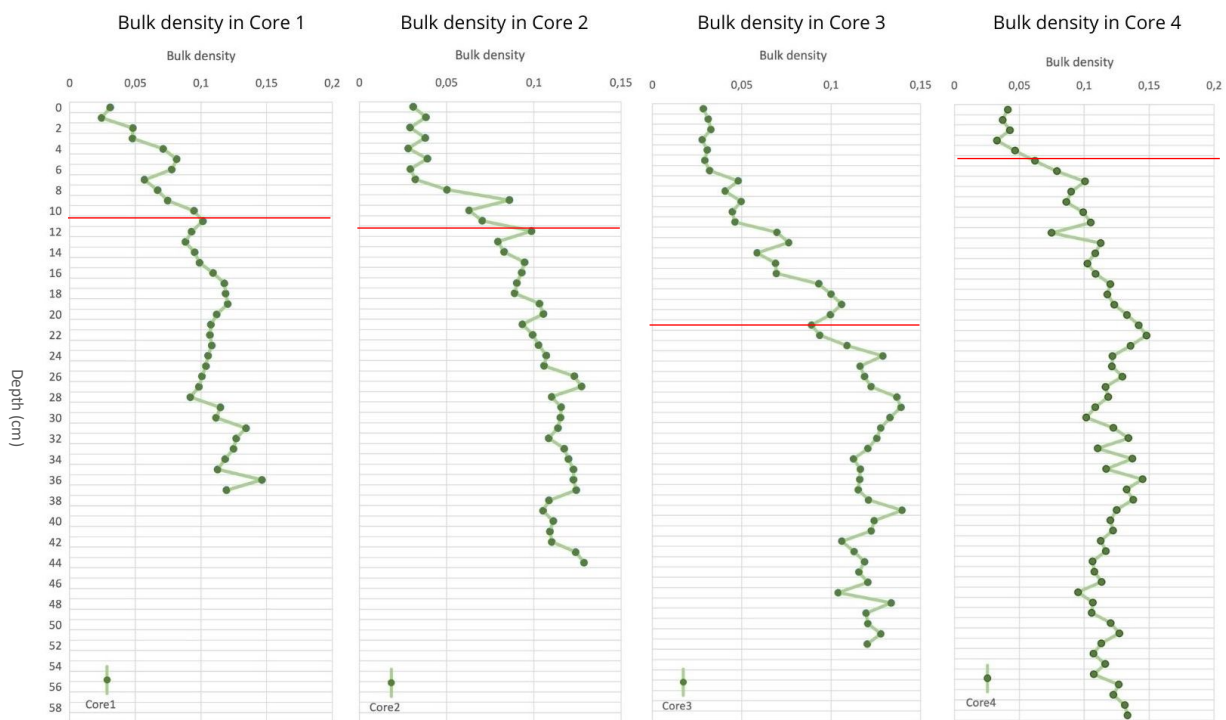


Figure 13. Bulk density (g/cm³) by depth in Cores 1-4. The red lines indicate the change from sedge peat to Sphagnum peat.

In all four cores, the C/N ratio increases towards the surface (Figure 14). The increase is rapid and follows the change in the peat type. The sedge peat has a rather steady C/N ratio around 20, but when the peat type changes into Sphagnum-peat, the C/N ratio rises typically to 40 – 70.

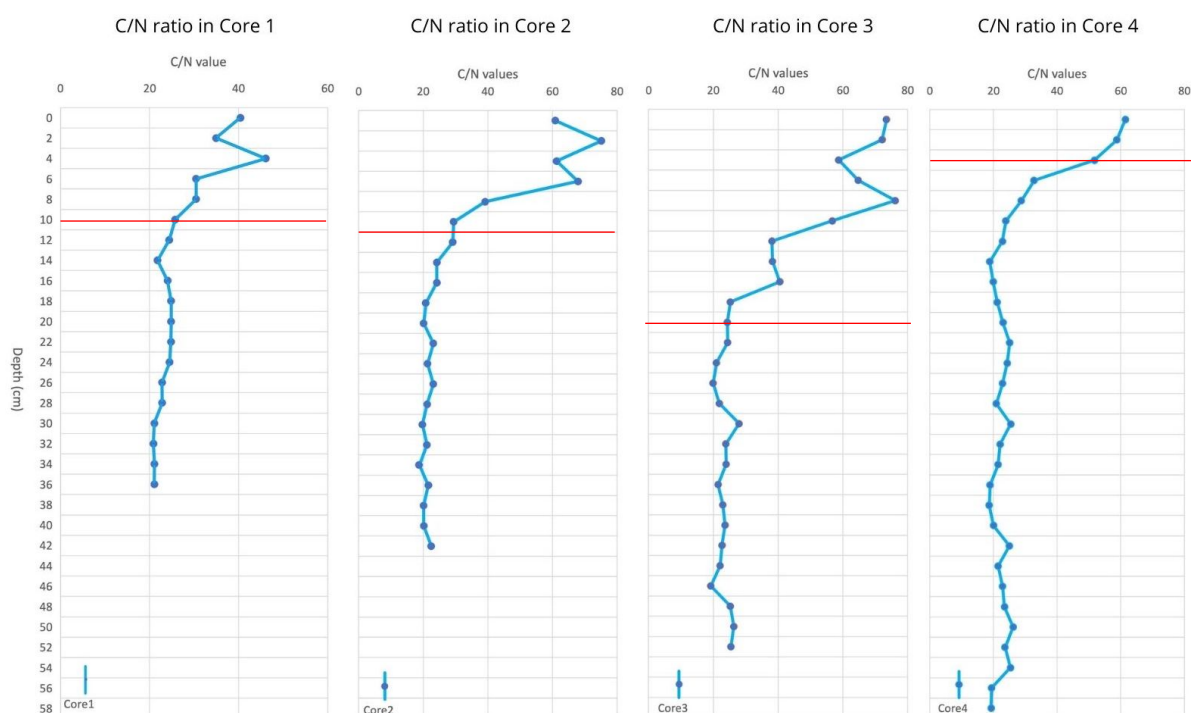


Figure 14. C/N ratio by depth in Cores 1-4. The red line indicates the change from sedge peat to Sphagnum peat.

3.4 Peat and carbon accumulation

The average peat accumulation rate from 1775 to 2020 was 2 mm/yr¹. ACAR and peat accumulation follow a similar pattern: there is an overall increasing trend, with particularly high values between the years 1944 and 1963 as well as during the past few years (Figures 15 & 16). However, the data point suggesting a sudden peak in the peat accumulation in 1944 – 1963 is an outlier likely explained by an erroneous dating result (Figures 8, 15 & 16). RERCA for the whole sequence 1775 – 2020 is 160 g C m²yr¹. Prior to the change from sedge- to Sphagnum-dominated vegetation, RERCA is 230 g C m²yr¹, whereas after the change it is 412 g C m²yr¹ (Table 3).

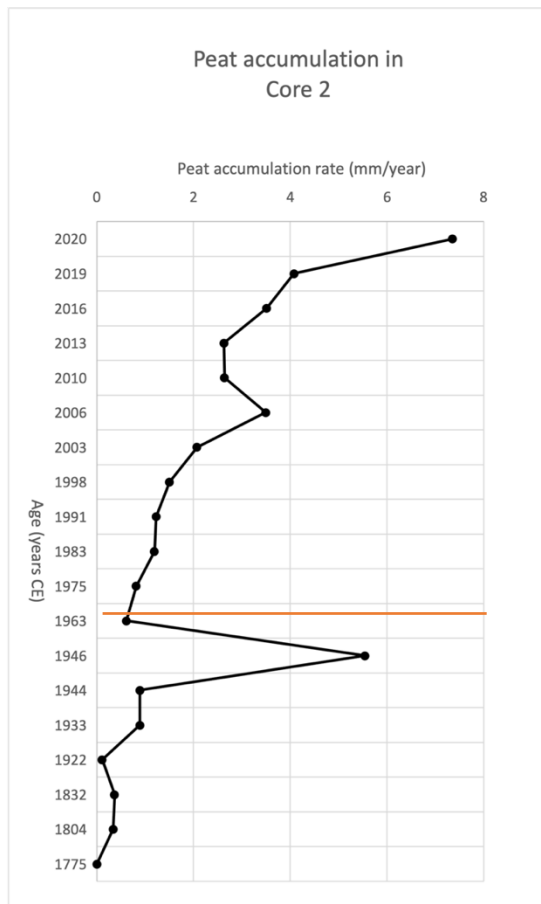


Figure 15. Peat accumulation rate in Core 2. The red line indicates the change from sedge peat (below) to *Sphagnum* peat (above).

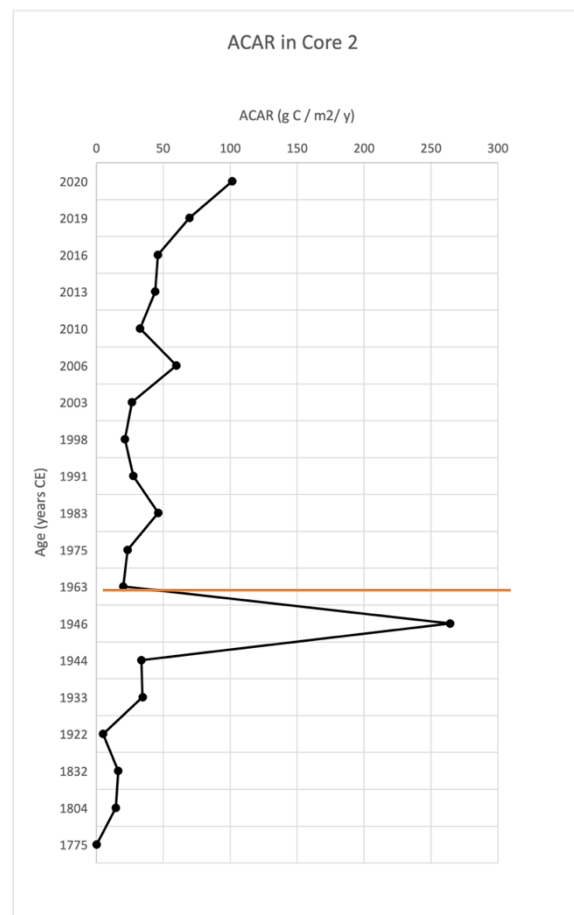


Figure 16. Apparent Carbon Accumulation Rate in Core 2. The red line indicates the change from sedge peat (below) to *Sphagnum* peat (above).

Table 3. Recent Apparent Carbon Accumulation Rate in Core 2.

	RERCA (g C/m ² /yr)
Total	161
<i>Sphagnum</i> peat	414
Sedge peat	230

4. Discussion

4.1 The vegetation shift at Lompolojänkä

Dryer and more oligotrophic conditions in the margins compared to central parts are typical for aapa mires (Rydin et al., 1999). However, a clear shift in the vegetation community of the marginal peatland area was detected in all four cores (Figures 9 – 12): the previous vegetation community in the margins resembles the current community in the central areas of the fen. The high share of *Cyperaceae*, as well as the presence of *Calliergon sp.* and *Sphagnum cf. majus* (in Core 4), indicate that relatively wet conditions have persisted until around the early 1960s when the rapid change occurred (Figure 10). Accordingly, it seems likely that the shift occurred only after the ongoing warming had begun. The expansion of *Acutifolia*-type *Sphagna*, accompanied by a few other moss species and the disappearance of *Cyperaceae*, indicates a shift towards dryer and/or more oligotrophic conditions, as if the vegetation typical for mire margins was expanding towards the centre. Cores 1 and 2 show a *Pleurozium schreberi* – phase from the 1980s to the beginning of the 1990s, which is a clear sign of dry conditions: *Pleurozium schreberi* is commonly found in forests and occupies only the driest hummocks on peatlands (Laine et al., 2018).

Sphagnum fuscum – the dominant species in Cores 1, 2, and 3 – is not only an indicator of dry but also ombrotrophic conditions (Laine et al., 2018). Ombrotrophication is often detected as a shift from sedge peat to *Sphagnum* peat within decades or centuries. Besides the vertical peat growth, ombrotrophication may be triggered by a water table draw-down that isolates the peatland surface from minerogenic water sources (Hughes & Barber, 2004; Tahvanainen, 2011). However, *Sphagnum warnstorffii* is highly abundant in the study site, dominating the surface of Core 4 and surrounding the *Sphagnum fuscum* hummocks (Figure 12, personal observation 2020). *Sphagnum warnstorffii* is an indicator of the presence of a minerogenic water source (Laine et al., 2018). Even if a local lack of nutrients was prevailing at the marginal areas of the peatland, ecosystem-scale ombrotrophication of Lompolojänkä in the nearby future seems unlikely, as there is currently a stream flowing through the peatland and the vegetation shows no signs of the lack of nutrients in the central parts of the peatland. Thus, it seems likely that the observed vegetation change has been triggered by at least one allogenic factor.

The ongoing warming trend began in Finnish Lapland after Little Ice Age (LIA), in the mid-19th – early 20th century (Helama et al., 2009a; Luoto et al., 2017). Throughout the 20th century, the warming climate trend has prevailed. 1920s and 1930s were particularly warm in Finnish

Lapland, mostly due to increasing summer temperatures (Lee et al., 2000; Helama et al., 2009a; Luoto et al., 2017). Even though the most drastic warming period ended prior to the observed vegetation shift, the plant communities may have responded to the warmth with some delay. Similar shifts from wet *Sphagna* and fen vegetation into a *Sphagnum fuscum*-community have occurred during MCA (Zhang, 2018b), which was a relatively warm and dry period in Northern Fennoscandia (Helama et al., 2009b; Linderholm et al., 2018). Thus, it is likely that the vegetational shift occurring at the beginning 1960s is a response to the current warming.

The paleovegetation of Lompolojänkkä has been investigated by Niemelä (2012). Her findings did not indicate such a drastic change in vegetation composition that was visible in my results. On the contrary, she found the amount of *Cyperaceae* to increase towards the surface. However, her samples were cored from the central parts of the fen, whereas those of this study were from the marginal areas of the peatland. This supports the visual observations from the study site, according to which the change is only occurring in the marginal areas. A similar, recent expansion of hummock species – mainly *Sphagna* – has been observed in northern fens by Pedrotti et al. (2014) in South-Eastern Sweden and by Kolari et al. (2021) in Eastern Finland. Kolari et al. (2021) found a change in the vegetation of a fen margin within two decades in repeated sampling. Interestingly, they did not find a notable overall decrease in the water table level in repeated measurements – instead, the vegetation change was interpreted to be caused by increased *Sphagnum* growth triggered by the warming climate. As they justified, *Sphagna* may benefit from long and warm growing seasons as long as the moisture supply remains sufficient (Bengtsson et al., 2021). It seems possible that also at Lompolojänkkä the vegetation is responding directly to the increasing temperature rather than via changes in the local hydrology. However, *Sphagnum fuscum* – the dominant species in 3 of 4 cores – is not capable of taking the advantage of increased temperatures as efficiently as e.g. *Sphagnum magellanicum* (Bengtsson et al., 2021). Therefore, a change in the local hydrology at Lompolojänkkä cannot be ruled out with certainty.

4.2 Carbon dynamics at Lompolojänkkä

The Holocene-scale radiative forcing effect of Lompolojänkkä has been simulated by Mathijssen et al. (2014). Due to high CH₄ emissions, the net radiative forcing impact of Lompolojänkkä was positive during the early phase of its succession but shifted into negative as the total carbon accumulation exceeded the effect of CH₄ 5000 years ago or even earlier (Mathijssen et al., 2014). Based on three years of on-site measurements, Aurela et al. (2009) concluded that Lompolojänkkä functions as a net carbon sink and has a cooling impact on

climate. However, between the years 2007 and 2016, a hint of an increasing trend in ecosystem respiration has been observed, due to which the net annual carbon uptake has decreased (Lohila et al., 2018). Despite the change towards drought-adapted communities in Lompolojänkän margins, the water table level remained high in the central parts of the fen even during the extremely warm and dry summer of 2018. Together with the increased peat temperature, it caused exceptionally high CH₄ emissions (Rinne et al. 2020).

According to the plant macrofossil data, the shift towards *Sphagnum*-dominated plant communities in the mire margins occurred already in the 1960s. Thus, the observed vegetation shift does not directly explain the measured decrease in carbon uptake in 2007 – 2016. However, even though no signs of drying have been detected from the central parts of the peatland, one must bear in mind that the vegetation may respond to environmental changes with some delay. Also, Lompolojänkän is highly heterogenous and hosts several different plant community types. Thus, should there be a very recent drying in the central areas of the peatland, it may not have been visible yet in the previous field campaigns. As decreasing carbon accumulation has been associated with past warm periods on Lompolojänkän and other subarctic fens (Borren et al., 2004; Jones et al., 2009; Mathijssen et al., 2014), the recently decreased carbon uptake may be a response to the warming climate. However, according to the peat analyses, the carbon accumulation seems not to have decreased at Lompolojänkän fen margins towards the present.

The lowest carbon accumulation rate was detected between the years 1832 and 1922 when only 1 cm of peat was accumulated in 90 years (Figure 8). This is possibly due to Little Ice Age (LIA), a cool climate period that persisted until the early 20th century in Finnish Lapland (Helama et al., 2009a; Luoto et al., 2017). Contrastingly, high peat and carbon accumulation rates during LIA have been reported from other subarctic fens, but those have likely been affected by permafrost dynamics and/or a shift to *Sphagnum*-dominated communities (Zhang, 2018a; Piilo et al., 2020). In permafrost-free peatlands, decreasing carbon accumulations during LIA have been reported by Charman et al. (2013).

The carbon accumulation rates of Lompolojänkän show an increasing trend towards the present. RERCA for the whole dated peat section is 160 g C/m²/yr¹. This is slightly higher compared to most subarctic fens: Piilo et al. (2019) reported RERCA ranging from 50.7 to 149.1 g C/m²/yr¹, and Turunen (2003) from 30 to 120 g C/m²/yr¹. RERCA is notably higher for the *Sphagnum*-dominated section compared to the sedge-dominated section (Table 3). This could result from the shift into a *Sphagnum*-dominated community, as *Sphagnum* mosses are known to increase

carbon accumulation rates (Turunen, 2003; Tuittila et al., 2013). However, it is also possible that the increasing RERCA is simply due to incomplete decomposition processes of the fresh peat (e.g. Young et al., 2019). Young et al. (2021) concluded that ACAR and RERCA are not reliable proxies when comparing past and present carbon accumulation rates. This is because of the incomplete decomposition, and the fact that these calculations ignore the processes that may have occurred in deeper peat layers simultaneously with the accumulation on the surface. Thus, it must be borne in mind that ACAR and RERCA do not fully describe the carbon balance of the peatland at a given time. However, there is also a drastic increase in the C/N ratios following the change in the peat type. This indicates that the changing vegetation type plays a role in the observed carbon accumulation change.

4.3 Future research

My results together with the contrasting observations from Lompolojänkää (Niemelä, 2012; Mathijssen et al., 2014; Rinne et al., 2020) highlight that peatland climate responses may vary even within an individual peatland. In this case, the vegetation on the fen margins has shifted towards more drought-adapted and oligotrophic communities even though water table decline or vegetation changes have not been observed in the central areas of the peatland. Similar conclusions have been made by Zhang et al. (2018a), Piilo et al. (2020), and Kolari et al. (2021) from other fens in Finland and Russia.

Peatland climate response depends on a complicated set of allogenic and autogenic drivers, and as peatland coverage in the northern hemisphere is as high as 3.7 ± 0.5 million km² (Hugelius et al., 2020), this poses further challenges for forming a coherent understanding of their future. Thus, more research is required before anything can be generalized for vast areas. There is a need for both increasing spatial coverage of the data and the multi-core approach within an individual peatland. The versatility of different methods should be considered when planning future research approaches. Using a multi-proxy approach would increase the accuracy of the results. For instance, it would be interesting to investigate testate amoebae communities in Lompolojänkää and see what kind of hydrological changes they indicate in both the peatland margins and the central area. Testate amoebae are a powerful proxy for past water table fluctuations, and they respond to environmental changes within a shorter time compared to plants (Väliiranta et al., 2012). Thus, were there any recent – even minor – hydrological changes in the central parts of Lompolojänkää, they could be reflected by testate amoebae, even though the change is not visible in the plant community.

4.4 Uncertainties and potential sources of error

The methods applied in this study are traditional and highly accepted by the scientific community. The necessity of multiple coring points has been recognized in previous palaeoecological studies (e.g. Piilo et al., 2020) as it significantly increases the reliability of the results and benefits data interpretation. However, certain sources of uncertainty still exist. My results represent only the marginal areas of Lompolojänkki, thus I cannot generalise them for the whole peatland. Currently, the vegetation of Lompolojänkki peatland is highly heterogeneous. My results prove that there have been some differences in the vegetation communities also in the past. For instance, Core 4 seems to have been a relatively wet habitat throughout the covered time, whereas the other three cores show a higher number of shrubs and hummock mosses. However, despite the small differences, all four cores show a similar change from a *Cyperaceae*-dominated fen into a *Sphagnum*-dominated hummock or lawn. Thus, I can conclude with relatively high certainty that this change is truly occurring in the mire margins of Lompolojänkki.

I analysed plant macrofossils mainly at 4 cm resolution. This is high enough to capture major changes in the vegetation. However, short-term variation in the vegetation might have been unnoticed. Where a change was detected, I increased the sample resolution to one cm in order to investigate the change more accurately. Besides, in the plant macrofossil analysis, misleading results may originate from the roots of the modern vegetation penetrating into the deeper layers and differences in the decay rates between plant species (Mauquoy & van Geel, 2013). At the beginning of the analysis, my experience in plant macrofossil analysis was limited. However, the first and the most challenging samples were analysed under supervision. I also tested my skills by re-analysing the samples, which demonstrated to me that my skills had improved during the process and also made me more confident about my results. It should also be borne in mind that the visual estimation of the proportions of each species or plant type is always somewhat subjective.

Only one core, Core 2, was dated and the lead isotope method was used. According to the dating results, one cm of peat has been accumulated between the years 1944 and 1946 (Figure 8). This is a rather unrealistic value when comparing to the general peat accumulation rate of the peatland (Figure 8). No other explanation could not be thought of but an unfortunate error in the dating procedure. Thus, also the timing of the vegetational shift must be considered critically. The use of other, overlapping dating methods would be essential to improve the reliability of the chronology and results. Caesium and radiocarbon isotope methods were

considered as supplementary dating methods, but the strict timetable did not allow those to be performed. For the same reason, only one of the four cores was dated. The results would be better comparable with each other if all four cores had robust chronologies. However, the shift in the vegetation community is included in the dated section, and it occurs rather near the surface in all cores, so it can be assumed that the change has occurred approximately simultaneously in all four coring points and most likely only after the current warming began. The dating resolution was one cm, which is a relatively high resolution.

5. Conclusions

Warmer and dryer summers are expected in northern high latitudes in the future (Najafi et al., 2015; Overland et al., 2018). Peatland carbon dynamics are tightly connected to hydrology, which is affected by both climate and autogenic development of the peatland. This implies that further changes in the vegetation, hydrology, and carbon dynamics of northern peatlands are likely. Due to the complexity of peatland ecohydrology and carbon dynamics, predicting the future of the peatland carbon stock is challenging.

As shown in this thesis, peatland climate responses may vary even within a single peatland. To answer my first research question; a shift from a sedge-dominated into a *Sphagnum*-dominated community since the 1960s was detected in the marginal area of the peatland. However, the central part of the peatland remains a wetter fen. To answer the second research question; the shift into a *Sphagnum*-dominated community seems to have increased the carbon accumulation at the peatland margins, even though a decreased carbon uptake has been observed in ecosystem-scale measurements (Lohila et al., 2018). However, as explained by Young et al. (2021), peatland carbon accumulation rates should be considered critically.

Both the increasing temperature and permanent water table drawdown may trigger an expansion of *Sphagnum* at the cost of sedges (e.g. Bengtsson et al., 2021). This change likely decreases CH₄ emissions (Mäkiranta et al., 2018; Riutta et al. 2020) and possibly increases carbon accumulation (Turunen, 2003; Tuittila et al., 2013), which would have a cooling climate impact. In case peatlands are drying, several consequences are possible, and the net climate impact depends on which of those are the most prominent. Drying and warming conditions may inhibit photosynthesis and increase oxic decomposition, which would result in a smaller carbon sink and increasing CO₂ emissions (Aurela et al., 2009; Laine et al., 2019). The decrease of water tables is also known to decrease CH₄ emissions, which has a cooling impact on climate

(Nykänen et al., 1998; Riutta et al., 2020). On the other hand, an increasing amount of CH₄ may be emitted from wet northern peatlands that have special hydrological features ensuring a constant water supply even during extreme heatwaves and droughts (Rinne et al., 2020).

To conclude, multiple different changes are likely occurring simultaneously in northern fens. Local topography and hydrology may play a central role in determining the development of a peatland's carbon dynamics, but the vegetation may also respond directly to the increased temperature. Some consistency between sites has been detected: recent peatland drying has been reported from Northern Fennoscandia (Galka et al., 2017; Piilo; 2017), Russia (Zhang et al., 2018b), Canada (Bellen et al., 2018), and even boreal and temperate peatlands (Swindles et al., 2019; Zhang et al., 2020). The expansion of *Sphagna* similar to this study was found to be due to temperature increase in Eastern Finland by Kolari et al. (2021). To form a more coherent understanding of the peatland climate responses, i.e., the fate of the remarkable carbon stock they maintain, further research with high spatial coverage, multi-core approach, and versatile methods is crucial.

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References

- Alm, J., Saarnio, S., Nykänen, H., Silvola, J. & Martikainen, P.J. (1999). "Winter CO₂ CH₄ and N₂O fluxes on some natural and drained boreal peatlands. *Biogeochemistry*, vol. 44, no. 2, pp. 163-186.
- Appleby P. G. & Oldfield F. R. (1978). The calculation of ²¹⁰Pb dates assuming a constant rate of supply of unsupported ²¹⁰Pb to the sediment. *Catena (Supplement)*, 5:1-8.
- Aurela, M., Laurila, T. & Tuovinen, J.-P. (2004). The timing of snow melt controls the annual CO₂ balance in a subarctic fen. *Geophysical Research Letters* 31, L16119, doi:10.1029/2004GL020315.
- Aurela M, Lohila A, Tuovinen J-P et al. (2009). Carbon dioxide exchange on a northern boreal fen. *Boreal Environment Research* 14: 699–710.
- Ballantyne, D.M., Hribljan, J.A., Hribljan, J.A., Pypker, T.G., Pypker, T.G., Chimner, R.A. & Chimner, R.A. (2014). Long-term water table manipulations alter peatland gaseous carbon fluxes in Northern Michigan. *Wetlands Ecology and Management*, vol. 22, no. 1, pp. 35-47.
- Barber, K. Chambers, F.M., Maddy, D., Stoneman, R.E., Brew, J.S. (1994). A sensitive high-resolution record of late-Holocene climatic change from a raised bog in northern England. *The Holocene*, 4, pp. 198-205
- Bellen, S., Magnan, G., Davies, L., Froese, D., Mullan-Boudreau, G., Zaccane, C., Garneau, M., & Shotyk, W. (2018). Testate amoeba records indicate regional 20th-century lowering of water tables in ombrotrophic peatlands in central-northern Alberta, Canada. *Global Change Biology*, 24(7), 2758–2774. <https://doi.org/10.1111/gcb.14143>
- Bellisario, L.M., Bubier, J.L., Moore, T.R. & Chanton, J.P. (1999). Controls on CH₄ emissions from a northern peatland. *Global Biogeochemical Cycles*, vol. 13, no. 1, pp. 81-91.
- Bengtsson, F., Rydin, H., Baltzer, J. L., Bragazza, L., Bu, Z. J., Caporn, S. J., & Ganeva, A. (2021). Environmental drivers of Sphagnum growth in peatlands across the Holarctic region. *Journal of Ecology*. 109(1), 417–431. <https://doi.org/10.1111/1365-2745.13499>
- Bergman, I., Svensson, B.H. & Nilsson, M. (1998). Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. *Soil Biology and Biochemistry*, vol. 30, no. 6, pp. 729-741.
- Birks, H.H. (2013) Plant macrofossil introduction. In: Elias, S.A. (ed.) *Encyclopedia of Quaternary Science, Volume 3*. Elsevier, Amsterdam, 2266– 2288.
- Borren, W., Bleuten, W. & Lapshina, E.D. (2004). Holocene peat and carbon accumulation rates in the southern taiga of western Siberia. *Quaternary Research* 61: 42–51.
- Bubier, J., & Moore, T. (1994). An ecological perspective on methane emissions from northern wetlands. *Trends in Ecology & Evolution*, 9(12), 460–464. [https://doi.org/10.1016/0169-5347\(94\)90309-3](https://doi.org/10.1016/0169-5347(94)90309-3)
- Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola,

- A., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, A., Swindles, G.T., Tuittila, E., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D.H. & Zhao, Y. (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, vol. 10, no. 2, pp. 929-944.
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R.B., Piao, S., & Thornton, P. (2013). Carbon and other biogeochemical cycles: Supplementary material. In Stocker, T.F., Qin, G.-K., Plattner, M., Tignor, S.K., Allen, J., Boschung, A., Nauels, Y., Xia, V. Bex & P.M. (Eds.): *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, 465-570.
- Clymo R.S. (1964). The origin of acidity in Sphagnum bogs. *Bryologist* 67: 427-431
- Clymo, R.S. (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. Biological Sciences*, 303(1117), 605-654. <https://doi.org/10.1098/rstb.1984.0002>
- Colmer, T.D. (2003). Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell & Environment*, 26: 17-36. <https://doi.org/10.1046/j.1365-3040.2003.00846.x>
- Conner, L. G., Gill, R. A. & Belnap, J. (2016). Soil moisture response to experimentally-altered snowmelt timing is mediated by soil, vegetation, and regional climate patterns. *Ecohydrology*, 9:1006-101
- Drewer, J., Lohila, A., Aurela, M., Laurila, T., Minkkinen, K., Penttilä, T., Dinsmore, K.J., McKenzie, R.M., Helfter, C., Flechard, C., Sutton, M.A. & Skiba, U.M. (2010). Comparison of greenhouse gas fluxes and nitrogen budgets from an ombrotrophic bog in Scotland and a minerotrophic sedge fen in Finland. *European Journal of Soil Science*, vol. 61, no. 5, pp. 640-650.
- Dunfield, P., Knowles, R., Dumont, R. & Moore, T.R. (1993). Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH. *Soil biology & biochemistry*, vol. 25, no. 3, pp. 321-326.
- Frolking, S. & Roulet, N.T. (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, vol. 13, no. 5, pp. 1079-1088.
- Fyfe, J.C., von Salzen, K., Gillett, N.P., Arora, V.K., Flato, G.M. & McConnell, J.R. (2013). One hundred years of Arctic surface temperature variation due to anthropogenic influence. *Scientific reports; Sci Rep*, vol. 3, no. 1, pp. 2645.
- Gałka, M., Szal, M., Watson, E.J., Gallego-Sala, A., Amesbury, M.J., Charman, D.J., Roland, T.P., Edward Turner, T. & Swindles, G.T. (2017) Vegetation Succession, Carbon Accumulation and Hydrological Change in Subarctic Peatlands, Abisko, Northern Sweden: Vegetation Succession and Carbon Accumulation Dynamics. *Permafrost and Periglacial Processes*, vol. 28, no. 4, pp. 589-604.

- Gallego-Sala, A., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S., Blyakharchuk, T., Bochicchio, C., Booth, R.K., Bunbury, J., Camill, P., Carless, D., Chimner, R.A., Clifford, M., Cressey, E., Courtney-Mustaphi, C., De Vleeschouwer, F., de Jong, R., Fialkiewicz-Koziel, B., Finkelstein, S.A., Garneau, M., Githumbi, E., Hribljan, J., Holmquist, J., Hughes, P.D.M., Jones, C., Jones, M.C., Karofeld, E., Klein, E.S., Kokfelt, U., Korhola, A., Lacourse, T., Le Roux, G., Lamentowicz, M., Large, D., Lavoie, M., Loisel, J., Mackay, H., MacDonald, G.M., Makila, M., Magnan, G., Marchant, R., Marcisz, K., Martínez Cortizas, A., Massa, C., Mathijssen, P., Mauquoy, D., Mighall, T., Mitchell, F.J.G., Moss, P., Nichols, J., Oksanen, P.O., Orme, L., Packalen, M.S., Robinson, S., Roland, T.P., Sanderson, N.K., Sannel, A.B.K., Silva-Sánchez, N., Steinberg, N., Swindles, G.T., Turner, T.E., Uglow, J., Väliranta, M., van Bellen, S., van der Linden, M., van Geel, B., Wang, G., Yu, Z., Zaragoza-Castells, J. & Zhao, Y. (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nature climate change*, vol. 8, no. 10, pp. 907-913.
- Gibson, C., Chasmer, L., Thompson, D., Quinton, W., Flannigan, M., & Olefeldt, D. (2018). Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature Communications*, 9(1), 3041–3041. <https://doi.org/10.1038/s41467-018-05457-1>
- Gong J., Kellomäki S., Wang K., Zhang C., Shurpali N. & Martikainen P. J. (2013): Modeling CO₂ and CH₄ flux changes in pristine peatlands of Finland under changing climate conditions. *Ecological Modelling*, 263: 64-80.
- Gorham, E. (1991). Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications*; Ecol Appl, vol. 1, no. 2, pp. 182-195.
- Heiskanen, L., Tuovinen, J., Räsänen, A., Virtanen, T., Juutinen, S., Lohila, A., Penttilä, T., Linkosalmi, M., Mikola, J., Laurila, T., & Aurela, M. (2021). Carbon dioxide and methane exchange of a patterned subarctic fen during two contrasting growing seasons. *Biogeosciences*, 18(3), 873–896. <https://doi.org/10.5194/bg-18-873-2021>
- Helama, S., Makarenko, N., Karimova, L., Kruglun, O., Timonen, M., Holopainen, J., Meriläinen, J., & Eronen, M. (2009a). Dendroclimatic transfer functions revisited: Little Ice Age and Medieval Warm Period summer temperatures reconstructed using artificial neural networks and linear algorithms. *Annales Geophysicae*. 27. 10.5194/angeo-27-1097-2009
- Helama, S., Meriläinen, J., & Tuomenvirta, H. (2009b). Multicentennial megadrought in northern Europe coincided with a global El Niño-Southern Oscillation drought pattern during the Medieval Climate Anomaly. *Geology (Boulder)*, 37(2), 175–178. <https://doi.org/10.1130/G25329A.1>
- Helbig, M., Waddington, J., Alekseychik, P., Amiro, B., Aurela, M., Barr, A., Black, T., Blanken, P., Carey, S., Chen, J., Chi, J., Desai, A., Dunn, A., Euskirchen, E., Flanagan, L., Forbrich, I., Friborg, T., Grelle, A., Harder, S., ... Isabelle, P. (2020). Increasing contribution of peatlands to boreal evapotranspiration in a warming climate. *Nature Climate Change*, 10(6), 555–560. <https://doi.org/10.1038/s41558-020-0763-7>
- Hugelius, G., Loisel, J., Chadburn, S., Jackson, R., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M., Treat, C., Turetsky, M., Voigt, C., & Yu, Z. (2020). Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proceedings of the National Academy of Sciences - PNAS*, 117(34), 20438–20446. <https://doi.org/10.1073/pnas.1916387117>

- Hughes, P., & Barber, K. (2004). Contrasting pathways to ombrotrophy in three raised bogs from Ireland and Cumbria, England. *Holocene* (Sevenoaks), 14(1), 65–77. <https://doi.org/10.1191/0959683604hl690r>
- Huttunen, J.T., Nykänen, H., Turunen, J. & Martikainen, P.J. (2003) Methane emissions from natural peatlands in the northern boreal zone in Finland, Fennoscandia. *Atmospheric environment* (1994), vol. 37, no. 1, pp. 147-151.
- Ingram, H. (1978). Soil layers in mires: function and terminology. *Journal of Soil Science*, 29(2), 224–227. <https://doi.org/10.1111/j.1365-2389.1978.tb02053.x>
- Jones M.C., Peteet D.M., Kurdyla, D. et al. (2009). Climate and vegetation history from a 14,000-year peatland record, Kenai Peninsula, Alaska. *Quaternary Research* 72: 207–217.
- Juutinen, S., Väiliranta, M., Kuutti, V., Laine, A., Virtanen, T., Seppä, H., Weckström, J., & Tuittila, E. (2013). Short-term and long-term carbon dynamics in a northern peatland-stream-lake continuum: A catchment approach. *Journal of Geophysical Research. Biogeosciences*, 118(1), 171–183. <https://doi.org/10.1002/jgrg.20028>
- Kokkonen, N.A.K., Laine, A.M., Laine, J., Vasander, H., Kurki, K., Gong, J., Tuittila, E. & Collins, B. (2019). Responses of peatland vegetation to 15-year water level drawdown as mediated by fertility level. *Journal of vegetation science*, vol. 30, no. 6, pp. 1206-1216.
- Kolari, T. H. M., Korpelainen, P., Kumpula, T., & Tahvanainen, T. (2021). Accelerated vegetation succession but no hydrological change in a boreal fen during 20 years of recent climate change. *Ecology and Evolution*, 11(12), 7602–7621. <https://doi.org/10.1002/ece3.7592>
- Končalová, H. (1990). Anatomical adaptations to waterlogging in roots of wetland graminoids: limitations and drawbacks. *Aquatic Botany*, vol. 38, no. 1, pp. 127-134.
- Korhola, A. (1992). Mire induction, ecosystem dynamics and lateral extension on raised bogs in the southern coastal area of Finland. *Geographical Society of Finland*.
- Korhola, A., Ruppel, M., Seppä, H., Väiliranta, M., Virtanen, T. & Weckström, J. (2010) The importance of northern peatland expansion to the late-Holocene rise of atmospheric methane. *Quaternary science reviews*, vol. 29, no. 5, pp. 611-617.
- Krishnaswamy, S., Lal, D., Martin, J., & Meybeck, M. (1971). Geochronology of lake sediments. *Earth and Planetary Science Letters*, 11(1), 407–414. [https://doi.org/10.1016/0012-821X\(71\)90202-0](https://doi.org/10.1016/0012-821X(71)90202-0)
- Kultti, S., Oksanen, P. & Valiranta, M. (2004). Holocene tree line, permafrost, and climate dynamics in the Nenets region, east European Arctic. *Canadian journal of earth sciences; Revue canadienne des sciences de la Terre*, vol. 41, no. 10, pp. 1141-1158.
- Laine, A.M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H. & Tuittila, E. (2019). Warming impacts on boreal fen CO₂ exchange under wet and dry conditions. *Global Change Biology; Glob Chang Biol*, vol. 25, no. 6, pp. 1995-2008.
- Laine, A., Riutta, T., Juutinen, S., Väiliranta, M. & Tuittila, E. (2009). Acknowledging the spatial heterogeneity in modelling/reconstructing carbon dioxide exchange in a northern aapa mire. *Ecological Modelling*, vol. 220, no. 20, pp. 2646-2655.

- Laine, J., Flatberg, K. I., Harju, P., Timonen, T., Minkkinen, K., Laine, A., Tuittila, E.-S. & Vasander, H. (2018). Sphagnum mosses – The Stars of European Mires. *University of Helsinki, Department of Forest Sciences, Sphagna Ky, Helsinki*, 326 pp.
- Laîné, A., Nakamura, H., Nishii, K. et al. (2014). A diagnostic study of future evaporation changes projected in CMIP5 climate models. *Clim Dyn* 42, 2745–2761. <https://doi.org/10.1007/s00382-014-2087-7>
- Larmola, T., Tuittila, E., Tirola, M., Nykänen, H., Martikainen, P.J., Yrjälä, K., Tuomivirta, T. & Fritze, H. (2010). The role of Sphagnum mosses in the methane cycling of a boreal mire. *Ecology* (Durham), vol. 91, no. 8, pp. 2356-2365.
- Lee, S., Press, M., & Lee, J. (2000). Observed climate variations during the last 100 years in Lapland, northern Finland. *International Journal of Climatology*, 20(3), 329–346. [https://doi.org/10.1002/\(SICI\)1097-0088\(20000315\)20:3<329::AID-JOC472>3.0.CO;2-L](https://doi.org/10.1002/(SICI)1097-0088(20000315)20:3<329::AID-JOC472>3.0.CO;2-L)
- Lelieveld, J., Crutzen, P.J. & Brühl, C. (1993). Climate effects of atmospheric methane, *Chemosphere (Oxford)*, vol. 26, no. 1, pp. 739-768.
- Leppälä, M., Kukko-Oja, K., Laine, J. & Tuittila, E.-S. (2008). Seasonal dynamics of CO₂ exchange during primary succession of boreal mires as controlled by phenology of plants. *Écoscience* (Sainte-Foy), vol. 15, no. 4, pp. 460-471.
- Leppälä, M., Oksanen, J. & Tuittila, E.-S. (2011). Methane flux dynamics during mire succession. *Oecologia*; *Oecologia*, vol. 165, no. 2, pp. 489-499.
- Limpens, J., Berendse, F., Blodau, C., Canadell, J. G., Freeman, C., Holden, J., Roulet, N., Rydin, H., & Schaepman-Strub, G. (2008). Peatlands and the carbon cycle: from local processes to global implications – a synthesis. *Biogeosciences*, 5, 1475–1491, <https://doi.org/10.5194/bg-5-1475-2008>.
- Linderholm, H.W., Nicolle, M., Francus, P., Gajewski, K., Helama, S., Korhola, A., Solomina, O., Yu, Z., Zhang, P., D'Andrea, W.J., Debret, M., Divine, D.V., Gunnarson, B.E., Loader, N.J., Massei, N., Seftigen, K., Thomas, E.K., Werner, J., Andersson, S., Berntsson, A., Luoto, T.P., Nevalainen, L., Saarni, S. & Väliranta, M. (2018). Arctic hydroclimate variability during the last 2000 years: current understanding and research challenges. *Climate of the past*, vol. 14, no. 4, pp. 473-514.
- Lique, C., Holland, M.M., Dibike, Y.B., Lawrence, D.M. & Screen, J.A. (2016). Modeling the Arctic freshwater system and its integration in the global system: Lessons learned and future challenges. *Journal of geophysical research*. *Biogeosciences*, vol. 121, no. 3, pp. 540-566.
- Lohila, A., Aurela, M., Hatakka, J., Tuovinen, J-P., Penttilä, T. & Laurila, T. (2018). Long-term GHG measurements at a northern boreal fen show stable CH₄ emissions, increasing soil respiration and endangered carbon uptake as climate is warming. *20th EGU General Assembly, EGU2018, Proceedings from the conference held 4-13 April, 2018 in Vienna, Austria*, p.15163
- Loisel, J., Yu, Z., Beilman, D.W., Camill, P., Alm, J., Amesbury, M.J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L.R., Bunbury, J., Chambers, F.M., Charman, D.J., De Vleeschouwer, F., Fiałkiewicz-Kozieł, B., Finkelstein, S.A., Gałka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M.C., Klein, E.S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., Macdonald, G., Magnan, G., Mäkilä, M., Mallon, G., Mathijssen, P.,

- Mauquoy, D., McCarroll, J., Moore, T.R., Nichols, J., O'Reilly, B., Oksanen, P., Packalen, M., Peteet, D., Richard, P.J.H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A.B.K., Tarnocai, C., Thom, T., Tuittila, E.S., Turetsky, M., Välranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D., Zhao, Y. & Zhou, W. (2014). A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *Holocene* (Sevenoaks), vol. 24, no. 9, pp. 1028-1042.
- Loisel, J. & Yu, Z. (2013). Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska: Recent peat carbon sequestration rates. *Journal of geophysical research. Biogeosciences*, vol. 118, no. 1, pp. 41-53.
- Loisel, J., Gallego-Sala, A., Amesbury, M., Magnan, G., Anshari, G., Beilman, D., Benavides, J., Blewett, J., Camill, P., Charman, D., Chawchai, S., Hedgpeth, A., Kleinen, T., Korhola, A., Large, D., Mansilla, C., Müller, J., van Bellen, S., West, J., ... Moore, T. (2020). Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*. <https://doi.org/10.1038/s41558-020-00944-0>
- Luoto, T., Kivilä, E., Rantala, M., & Nevalainen, L. (2017). Characterization of the Medieval Climate Anomaly, Little Ice Age and recent warming in Northern Lapland: The Medieval Climate Anomaly, Little Ice Age and recent warming. *International Journal of Climatology*, 37, 1257–1266. <https://doi.org/10.1002/joc.5081>
- MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C. & Velichko, A.A. (2006). Rapid early development of circumarctic peatlands and atmospheric CH₄ and CO₂ variations. *Science* (American Association for the Advancement of Science), vol. 314, no. 5797, pp. 285-288
- Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R. S., Hughes, M. K., Shindell, D., Ammann, C., Faluvegi, G. & Ni, F. (2009). Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. *Science* (American Association for the Advancement of Science). [Online] 326 (5957), 1256–1260
- Marcott, S.A. (2013). A reconstruction of regional and global temperature for the past 11,300 years. *Science* (New York, N.Y.), 339(6124), pp. 1198.
- Mathijssen P., Tuovinen J.-P., Lohila A., Aurela M., Juutinen S., Laurila T., Niemelä E., Tuittila E.-S. & Välranta M. (2014). Development, carbon accumulation, and radiative forcing of a subarctic fen over the Holocene. *The Holocene*, 24(9):1156-1166.
- Mathijssen, P. J. H., Kähkölä, N., Tuovinen, J., Lohila, A., Minkkinen, K., Laurila, T., & Välranta, M. (2017). Lateral expansion and carbon exchange of a boreal peatland in Finland resulting in 7000 years of positive radiative forcing. *Journal of Geophysical Research. Biogeosciences*, 122(3), 562–577. <https://doi.org/10.1002/2016JG003749>
- Mauquoy, D., & van Geel, B. (2013). Mire and Peat Macros. In *Encyclopedia of Quaternary Science* (Second Edition, pp. 637–656). Elsevier B.V. <https://doi.org/10.1016/B978-0-444-53643-3.00206-5>
- Moore, T.R. & Knowles, R. (1987). Methane and carbon dioxide evolution from subarctic fens. *Canadian Journal Of Soil Science*. 67(1): 77-81. <https://doi.org/10.4141/Cjss87-007>
- Myhre, G., Shindell, D., Bréon, F.-M. et al. (2013). Anthropogenic and natural radiative forcing. In: Stocker TF, Qin D, Plattner G-K et al. (eds) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report*

- of the Intergovernmental Panel on Climate Change. Cambridge; New York: Cambridge University Press, pp. 659–740.
- Mäkilä, M. & Moisanen, M. (2007). Holocene lateral expansion and carbon accumulation of Luovuoma, a northern fen in Finnish Lapland. *Boreas*, vol. 36, no. 2, pp. 198-210.
- Mäkiranta, P., Laiho, R., Mehtätalo, L., Straková, P., Sormunen, J., Minkkinen, K., Penttilä, T., Fritze, H. & Tuittila, E.-S. (2018). Responses of phenology and biomass production of boreal fens to climate warming under different water-table level regimes. *Global Change Biology*; *Glob Chang Biol*, vol. 24, no. 3, pp. 944-956.
- Najafi, M.R., Zwiers, F.W. & Gillett, N.P. (2015) Attribution of Arctic temperature change to greenhouse-gas and aerosol influences. *Nature climate change*, vol. 5, no. 3, pp. 246-249.
- Neef, L., van Weele, M. & van Velthoven, P. (2010). Optimal estimation of the present-day global methane budget. *Global Biogeochemical Cycles*, vol. 24, no. 4, pp. n/a.
- Niemelä, E. (2012). Pohjoisen aapasuon jääkaudenjälkeinen kehitys, hiilitaseet ja ilmastovaikutus. *Helsingin yliopisto*, Helsinki
- Nykanen, H., Alm, J., Silvola, J., Tolonen, K. & Martikainen, P.J. (1998). Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. *Global Biogeochemical Cycles*, vol. 12, no. 1, pp. 53-69.
- Overland, J., Dunlea, E., Box, J.E., Corell, R., Forsius, M., Kattsov, V., Olsen, M.S., Pawlak, J., Reiersen, L. & Wang, M. (2019). The urgency of Arctic change. *Polar science*, vol. 21, pp. 6-13.
- Pedrotti, E., Rydin, H., Ingmar, T., Hytteborn, H., Turunen, P., & Granath, G. (2014). Fine-scale dynamics and community stability in boreal peatlands: Revisiting a fen and a bog in Sweden after 50 years. *Ecosphere*, 5(10), 1–24. <https://doi.org/10.1890/ES14-00202.1>
- Piilo, S. (2017). Subarctic Peatland Dynamics During the past Centuries - Changes in Vegetation, Moisture Conditions and Peat and Carbon Accumulation. *Helsingin yliopisto*, Helsinki
- Piilo, S., Zhang, H., Garneau, M., Gallego-Sala, A., Amesbury, M., & Väiranta, M. (2019). Recent peat and carbon accumulation following the Little Ice Age in northwestern Québec, Canada. *Environmental Research Letters*, 14(7), 75002–. <https://doi.org/10.1088/1748-9326/ab11ec>
- Piilo, S., Korhola, A., Heiskanen, L., Tuovinen, J., Aurela, M., Juutinen, S., Marttila, H., Saari, M., Tuittila, E., Turunen, J. & Väiranta, M.,M. (2020) Spatially varying peatland initiation, Holocene development, carbon accumulation patterns and radiative forcing within a subarctic fen. *Quaternary science reviews*, vol. 248.
- Pirinen P., Simola H., Aalto J., Kaukoranta J.-P., Karlsson P. & Ruuhela R. 2012. Climatological statistics of Finland 1981–2010. Finnish Meteorological Institute Reports 2012:1.
- Renssen, H., Seppä, H., Crosta, X., Goosse, H. & Roche, D.M. (2012). Global characterization of the Holocene Thermal Maximum. *Quaternary science reviews*, vol. 48, pp. 7-19.
- Rinne, J., Tuovinen, J.-P., Klemetsson, L., Aurela, M., Holst, J., Lohila, A., Weslien, P., Vestin, P., Łakomiec, P., Peichl, M., Peichl, M., Tuittila, E.-S., Heiskanen, L., Laurila, T., Li, X., Alekseychik, P., Mammarella, I., Ström, L., Crill, P. & Nilsson, M.B. (2020). Effect of the 2018 European drought on methane and carbon dioxide exchange of northern mire

- ecosystems. *Philosophical Transactions of the Royal Society. Biological Sciences*, vol. 375, no. 1810, 20190517. <https://doi.org/10.1098/rstb.2019.0517>
- Riutta, T., Laine, J. & Tuittila, E.-S. (2007). Sensitivity of CO₂ Exchange of Fen Ecosystem Components to Water Level Variation. *Ecosystems* (New York), vol. 10, no. 5, pp. 718-733.
- Riutta, T., Korrensalo, A., Laine, A. M., Laine, J., & Tuittila, E.-S. (2020). Interacting effects of vegetation components and water level on methane dynamics in a boreal fen. *Biogeosciences*, 17(3), 727–740. <https://doi.org/10.5194/bg-17-727-2020>
- Rodhe, H. (1990). A Comparison of the Contribution of Various Gases to the Greenhouse Effect. *Science (American Association for the Advancement of Science)*; *Science*, vol. 248, no. 4960, pp. 1217-1219.
- Ruppel, M., Välranta, M., Virtanen, T., & Korhola, A. (2013). Postglacial spatiotemporal peatland initiation and lateral expansion dynamics in North America and northern Europe. *Holocene(Sevenoaks)*, 23(11), 1596–1606. <https://doi.org/10.1177/0959683613499053>
- Rydin, H., Sjörs, H. & Löfroth, M. (1999). 7. Mires. *Acta Phytogeographica Suecica*. 84. 91-112
- Rydin, H. & Jeglum, J.K. (2006). The biology of peatlands. *Oxford university press*.
- Scharlemann, J., Tanner, E., Hiederer, R. & Kapos, V. (2014). Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* 5, 81–91
- Svensson, G. (1988). Bog development and environmental conditions as shown by the stratigraphy of Store Mosse mire in southern Sweden. *Boreas*, 17(1), 89–111. <https://doi.org/10.1111/j.1502-3885.1988.tb00126.x>
- Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J., Lamentowicz, M., Turner, T.E., Gallego-Sala, A., Sim, T., Barr, I.D., Blaauw, M., Blundell, A., Chambers, F.M., Charman, D.J., Feurdean, A., Galloway, J.M., Gałka, M., Green, S.M., Kajukalo, K., Karofeld, E., Korhola, A., Lamentowicz, Ł., Langdon, P., Marcisz, K., Mauquoy, D., Mazei, Y.A., McKeown, M.M., Mitchell, E.A.D., Novenko, E., Plunkett, G., Roe, H.M., Schoning, K., Sillasoo, Ü, Tsyganov, A.N., van der Linden, M., Välranta, M. & Warner, B. (2019). Widespread drying of European peatlands in recent centuries. *Nature geoscience*, vol. 12, no. 11, pp. 922-928.
- Tahvanainen, T. (2011). Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. *The Journal of ecology*, vol. 99, no. 2, pp. 404-415.
- Treat, C., & Jones, M. (2018). Near-surface permafrost aggradation in Northern Hemisphere peatlands shows regional and global trends during the past 6000 years. *Holocene (Sevenoaks)*, 28(6), 998–1010. <https://doi.org/10.1177/0959683617752858>
- Treat, C., Jones, M., Brosius, L., Grosse, G., Walter Anthony, K., & Frohling, S. (2021). The role of wetland expansion and successional processes in methane emissions from northern wetlands during the Holocene. *Quaternary Science Reviews*, 257, 106864–. <https://doi.org/10.1016/j.quascirev.2021.106864>

- Tuittila, E-S., Välranta, M., Laine, J. & Korhola, A. (2007). Quantifying patterns and controls of mire vegetation succession in a southern boreal bog in Finland using partial ordinations. *Journal of Vegetation Science*, vol. 18, no. 6, pp. 891-902.
- Tuittila, E-S., Juutinen, S., Froking, S., Välranta, M., Laine, A.M., Miettinen, A., Seväkivi, M., Quillet, A. & Merilä, P. (2013) Wetland chronosequence as a model of peatland development: Vegetation succession, peat and carbon accumulation. *Holocene* (Sevenoaks), vol. 23, no. 1, pp. 25-35.
- Turetsky M. R., Manning S. W. & Wieder R. K. (2004): Dating recent peat deposits. *Wetlands, The Society of Wetland Scientists*, 24(2):324-356.
- Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H. & Kelman Wieder, R. (2008). Trade-Offs in Resource Allocation among Moss Species Control Decomposition in Boreal Peatlands. *The Journal of ecology*, vol. 96, no. 6, pp. 1297-1305.
- Turetsky, M.R., Kotowska, A., Bubier, J., Dise, N.B., Crill, P., Hornibrook, E.R.C., Minkinen, K., Moore, T.R., Myers-Smith, I.H., Nykänen, H., Olefeldt, D., Rinne, J., Saarnio, S., Shurpali, N., Tuittila, E., Waddington, J.M., White, J.R., Wickland, K.P. & Wilmking, M. (2014). A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. *Global Change Biology; Glob Chang Biol*, vol. 20, no. 7, pp. 2183-2197
- Turunen J., Pitkänen A., Tahvanainen T. & Tolonen K. (2001): Carbon accumulation in West Siberian mires, Russia
- Turunen, J., Tomppo, E., Tolonen, K. & Reinikainen, A. (2002). Estimating carbon accumulation rates of undrained mires in Finland—application to boreal and subarctic regions. *Holocene* (Sevenoaks), vol. 12, no. 1, pp. 69-80.
- Turunen, J. (2003). Past and present carbon accumulation in undisturbed boreal and subarctic mires: A review. *Suo*. 54. 15-28.
- Vasander, H. (1998): Suomen suot. *Suoseura ry*. Helsinki. 167.
- Vihma, T., Screen, J., Tjernström, M., Newton, B., Zhang, X., Popova, V., Deser, C., Holland, M. & Prowse, T. (2016). The atmospheric role in the Arctic water cycle: A review on processes, past and future changes, and their impacts. *Journal of geophysical research. Biogeosciences*, vol. 121, no. 3, pp. 586-620.
- Voigt, C., Lamprecht, R.E., Marushchak, M.E., Lind, S.E., Novakovskiy, A., Aurela, M., Martikainen, P.J. and Biasi, C. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. *Glob Change Biol*, 23: 3121-3138. <https://doi.org/10.1111/gcb.13563>
- Välranta, M., Korhola, A., Seppä, H., Tuittila, E., Sarmaja-Korjonen, K., Laine, J. & Alm, J. (2007). High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during the late Holocene: a quantitative approach. *Holocene* (Sevenoaks), vol. 17, no. 8, pp. 1093-1107.
- Välranta, M. M., Blundell, A., Charman, D., Karofeld, E., Korhola, A., Sillasoo, Ü., & Tuittila, E.-S. (2012). Reconstructing peatland water tables using transfer functions for plant macrofossils and testate amoebae: a methodological comparison. *Quaternary International*, 268, 34-43.

- Väli­ranta, M., Salonen, J., Heikkilä, M., Amon, L., Helmens, K., Klimaschewski, A., Kuhry, P., Kultti, S., Poska, A., Shala, S., Veski, S., & Birks, H. (2015). Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. *Nature Communications*, 6(1), 6809–6809. <https://doi.org/10.1038/ncomms7809>
- Väli­ranta, M., Salojärvi, N., Vuorsalo, A., Juutinen, S., Korhola, A., Luoto, M. & Tuittila, E.-S. (2017). Holocene fen–bog transitions, current status in Finland and future perspectives. *Holocene (Sevenoaks)*, vol. 27, no. 5, pp. 752–764.
- Warner, B.G., Clymo, R. S. & Tolonen, K. (1992). Peat accumulation at Point Escuminac, New Brunswick, supports decay hypothesis for North American mires. *Quaternary Research* 39, 245–248.
- Weber, C.A. (1902). Über die Vegetation und Entstehung des Hochmoors von Augstumal im Memeldelta mit vergleichenden Ausblicken auf andere Hochmoore der Erde. Verlagsbuchhandlung Paul Parey. Berlin, DE.
- Whiting, G.J. & Chanton, J.P. (2001). Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus B*, 53(5), 521–528. <https://doi.org/10.1034/j.1600-0889.2001.530501.x>
- Xu, Jiren & Morris, Paul & Liu, Junguo & Holden, Joseph. (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena*. 160. 134–140. [10.1016/j.catena.2017.09.010](https://doi.org/10.1016/j.catena.2017.09.010).
- Young, D., Baird, A., Charman, D., Evans, C., Gallego-Sala, A., Gill, P., Hughes, P., Morris, P., & Swindles, G. (2019). Misinterpreting carbon accumulation rates in records from near-surface peat. *Scientific Reports*, 9(1), 17939–8. <https://doi.org/10.1038/s41598-019-53879-8>
- Young, D., Baird, A., Gallego-Sala, A., & Loisel, J. (2021). A cautionary tale about using the apparent carbon accumulation rate (aCAR) obtained from peat cores. *Scientific Reports*, 11(1), 9547–9547. <https://doi.org/10.1038/s41598-021-88766-8>
- Yrjälä, K., Tuomivirta, T., Juottonen, H., Putkinen, A., Lappi, K., Tuittila, E., Penttilä, T., Minkkinen, K., Laine, J., Peltoniemi, K., & Fritze, H. (2011). CH₄ production and oxidation processes in a boreal fen ecosystem after long-term water table drawdown: CH₄ production and oxidation processes. *Global change biology*, 17(3), 1311–1320. <https://doi.org/10.1111/j.1365-2486.2010.02290.x>
- Zhang, Y., Renssen, H., Seppä, H. & Valdes, P.J. (2017) Holocene temperature evolution in the Northern Hemisphere high latitudes – Model-data comparisons. *Quaternary science reviews*. [Online] 173101–113.
- Zhang, H., Gallego-Sala, A., Amesbury, M., Charman, D., Piilo, S., & Väli­ranta, M. (2018a). Inconsistent Response of Arctic Permafrost Peatland Carbon Accumulation to Warm Climate Phases. *Global Biogeochemical Cycles*, 32(10), 1605–1620. <https://doi.org/10.1029/2018GB005980>
- Zhang, H., Piilo, S.R., Amesbury, M.J., Charman, D.J., Gallego-Sala, A. & Väli­ranta, M.M. (2018b). The role of climate change in regulating Arctic permafrost peatland hydrological and vegetation change over the last millennium. *Quaternary science reviews*, vol. 182, pp. 121–130.
- Zhang, H., Väli­ranta, M., Piilo, S., Amesbury, M.J., Aquino-Lopez, M., Roland, T.P., Salminen-Paatero, S., Paatero, J., Lohila, A. & Tuittila, E.-S. (2020). Decreased carbon

accumulation feedback driven by climate-induced drying of two southern boreal bogs over recent centuries. *Global change biology*. [Online] 26 (4), 2435–2448.